

Effects of atmospheric CO₂ variability of the past 800 ka on the biomes of Southeast Africa

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Abstract

Very little is known about the impact of atmospheric carbon dioxide pressure ($p\text{CO}_2$) on the shaping of biomes. The development of $p\text{CO}_2$ throughout the Brunhes Chron may be considered a natural experiment to elucidate relationships between vegetation and $p\text{CO}_2$. While the glacial periods show low to very low values (~ 230 – 220 to ~ 190 ppmv, respectively), the $p\text{CO}_2$ levels of the interglacial periods vary from intermediate to relatively high (~ 250 to \sim more than 270, respectively). To study the influence of $p\text{CO}_2$ on the Pleistocene development of SE African vegetation, we used the pollen record of a marine core (MD96-2048) retrieved from Maputo Bay south of the Limpopo River mouth in combination with stable isotopes and geochemical proxies. Applying endmember analysis, four pollen assemblages could be distinguished representing different biomes: heathland, mountain forest, shrubland and woodland. We find that the vegetation of the Limpopo River catchment and the coastal region of southern Mozambique is not only influenced by hydroclimate but ~~by~~ also by temperature and atmospheric $p\text{CO}_2$. Our results suggest that the extension of mountain forest occurred during those parts of the glacials when $p\text{CO}_2$ and temperatures were moderate and that only during the colder periods when atmospheric $p\text{CO}_2$ was low (less than 220 ppmv) open ericaceous vegetation including C4 sedges extended. The ~~either open ericaceous vegetation including C4 sedges or mountain forest depended on glacial $p\text{CO}_2$ levels, and that the~~ main development of woodlands in the area took place after the Mid-Brunhes Event (~ 430 ka) when interglacial $p\text{CO}_2$ levels regularly rose over 270 ppmv.

Keywords

Palynology, Pleistocene, Limpopo River catchment, atmospheric carbon dioxide, Mid-Brunhes Event

Short summary

Multiproxy study of marine sediments off the Limpopo River mouth spanning the Late Pleistocene reveals the impact of atmospheric carbon dioxide on the development of the vegetation of Southeast Africa and indicates changes in the interglacial vegetation before and after the Mid-Brunhes Event.

Highlight

A multiproxy study of marine sediments off the Limpopo River mouth spanning the Late Pleistocene reveals the impact of atmospheric carbon dioxide on the development of the vegetation of Southeast Africa and indicates changes in the interglacial vegetation before and after the Mid-Brunhes Event. The unique record of detailed vegetation change in SE Africa over the entire Brunhes Chron demonstrates the expansion of glacial vegetation in southern Africa when atmospheric CO₂ concentration was low and the development of miombo woodland in SE Africa during successive interglacials after the Mid-Brunhes Transition.

1 Introduction

2 Understanding the role of atmospheric carbon dioxide pressure ($p\text{CO}_2$) is paramount for the
3 interpretation of the of the paleo-vegetation record. The effects of low $p\text{CO}_2$ on glacial vegetation
4 have been discussed in a number of studies [Ehleringer et al. 1997, Jolly & Haxeltine 1997, Cowling &
5 Sykes 1999, Prentice & Harrison 2009, Prentice et al. 2017] predicting that glacial increases in C4
6 vegetation favored by low atmospheric CO_2 would have opened the landscape and lowered the tree
7 line. ~~Comparing records of this glacial C4-rich vegetation with modern analogues could have led to~~
8 ~~estimating more severe aridity than actually occurred during the Last Glacial Maximum. Comparing~~
9 ~~this open C4-rich vegetation with modern analogues would have led to an erroneous interpretation~~
10 ~~of the occurrence of arid-adapted vegetation.~~ These studies [opt cit.], however, mostly cover the
11 ~~Glacial-Holocene~~ last glacial-interglacial transition and do not examine periods with intermediate
12 $p\text{CO}_2$ such as during the early-Early Glacial (MIS 5a-d) or interglacials prior to 430 thousand years ago
13 (430 ka). Comparing the vegetation record of subsequent climate cycles showing different CO_2 levels
14 might help to better understand the effects of $p\text{CO}_2$ on the vegetation.

15 During the Brunhes Chron (past 780 ka) the length of the glacial cycles became much longer lasting
16 roughly 100 ka due to a strong non-linear response of the ice sheets to solar forcing [Mudelsee &
17 Stattegger 1997]. Model experiments of Ganopolski & Calov [2011] indicate that low atmospheric
18 CO_2 concentrations are a prerequisite for the long duration of the glacial cycles of the past 800 ka.
19 Then, roughly mid-way through the Brunhes Chron, the amplitude of the climate cycles shifted with a
20 change in the maximum CO_2 concentration during interglacials.

21 This so-called Mid-Brunhes Event (MBE) [Jansen et al. 1986] - also called Mid-Brunhes Transition -
22 occurred about 430 ka ago and marks the transition between interglacials characterized by rather
23 low atmospheric CO_2 around 240 ppm (parts of Marine Isotope Stages (MIS) 19, 17, 15, 13) to
24 interglacials in which CO_2 levels reached 270 ppmv or more (parts of MIS 11, 9, 7, 5, 1) [Lüthi et al.
25 2008, Bereiter et al. 2015]. ~~This~~ climate transition of the MBE has been extensively studied using
26 Earth ~~system-System~~ Models of Intermediate Complexity. Yin & Berger [2010] stress the importance
27 of forcing by austral summer insolation and Yin & Berger [2012] argue that the model vegetation
28 (tree-fraction) was forced by precession through precipitation at low latitudes. Both papers showing
29 the necessity to include the change in atmospheric CO_2 in its-the explanation of the MBE [Yin &
30 Berger, 2010, 2012]. Additionally, Yin & Berger [2010] stress the importance of austral summer
31 insolation, while Yin & Berger [2012] find that the modelled vegetation (tree-fraction) was forced by
32 precession through precipitation at low latitudes. However, Yin [2013], however, concludes that it is
33 not necessary to invoke an sudden event around 430 ka to explain the increased interglacial CO_2 ; the
34 differences between interglacials before and after the MBE can be explained by individual responses
35 in Southern Ocean ventilation and deep-sea temperature to various combinations of the
36 astronomical parameters. ~~However, On the other hand,~~ statistical analysis suggests a dominant role
37 of the carbon cycle, which changed preceding-over the Mid-Brunhes-TransitionMBE [Barth et al.
38 2018]. Paillard [2017] developed a conceptual model of orbital forcing of the carbon cycle in which
39 sea-level fluctuations and the effects on carbon burial are decisive during shifts in the climate
40 system. Further modelling by Bouttes et al. [2018] showed qualitative agreement with the paleodata
41 of pre- and post-MBE interglacials but largely underestimated the amplitude of the changes.
42 Moreover, the simulated vegetation seems to counteract the effects of the oceanic response
43 [Bouttes et al. 2018]. Thus the vegetation, in particular at low latitudes, may play a crucial but poorly
44 understood role in the climate system.

Comparing records of pre- and post-MBE interglacials could offer insight in the interglacial climate at different levels of CO₂ and the dynamical response of the vegetation, which has a positive feedback with temperature via land surface albedo and evapotranspiration [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 pollen-vegetation records covering the entire Brunhes Chron have sufficient temporal resolution to enable comparisons

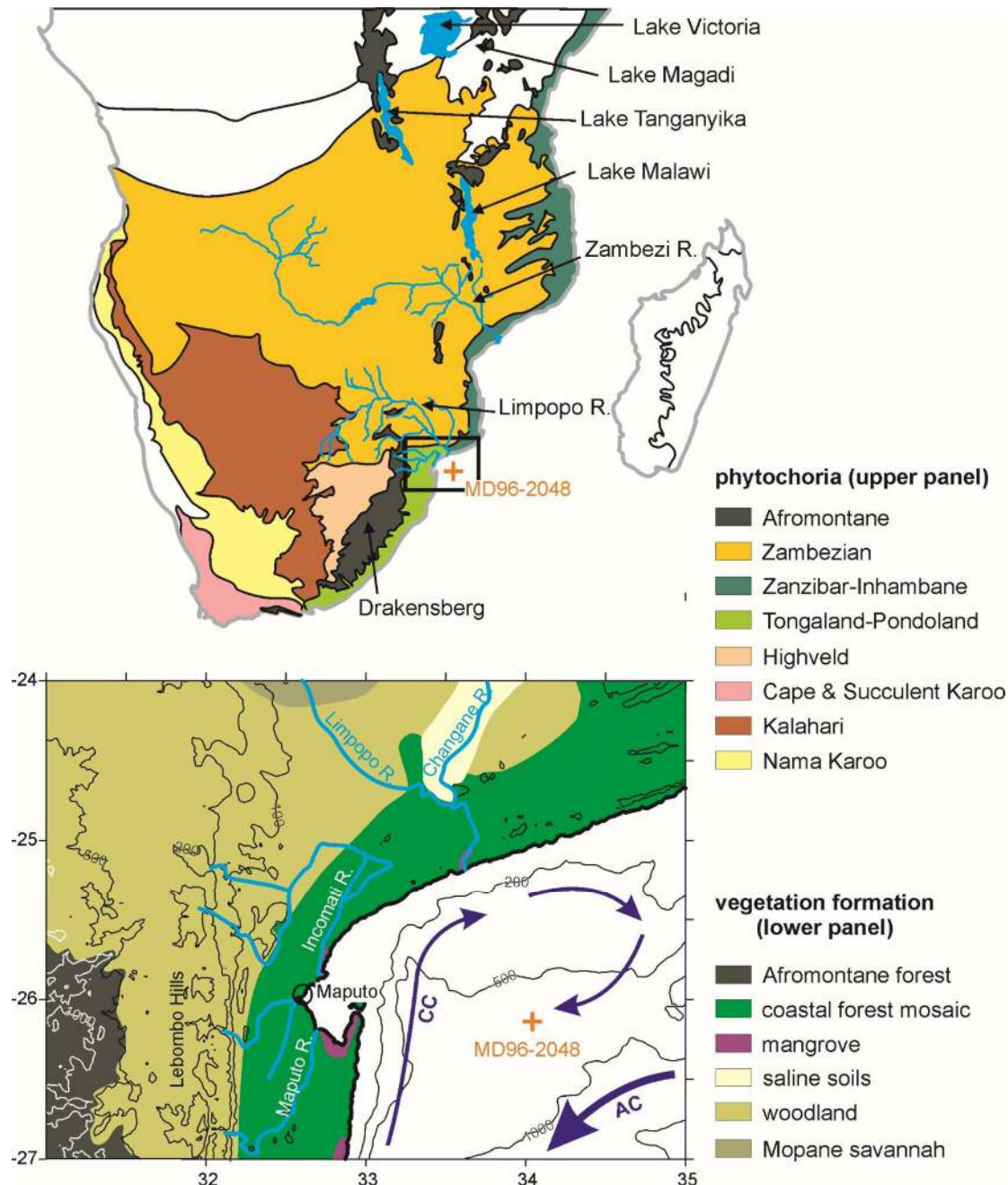


Figure 1. Upper panel: map of southern Africa with the main phytochoria after White (1983). Lower panel: site location of MD96-2048; main vegetation formations; main rivers; 100 m, 200 m, 500 m, and 1000m contours; 200 m, 500 m, and 1000m bathymetric contours; Agulhas (AC) and counter currents (CC) forming a coastal Maputo Bight Lee Eddy. Zambezian vegetation woodland and savannah north of ~25°30'S, Tongaland-Pondoland coastal forests south of ~25°30'S, Zanzibar-Inhambane coastal forests east of 33–34°E. West of the escarpment with Afromontane forest rises the interior plateau covered with Highveld grasslands rises.

between interglacials before and after the Mid-Brunhes transition. These records are from the eastern Mediterranean, ~~arctic Siberia~~, 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) ~~with where~~ the ~~modern Mediterranean oak forests~~ gradual emergence ~~in the interglacials of modern Mediterranean oak forests~~ 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 glacial 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. The El'gygytgyn vegetation record in eastern Siberia—resolved for MIS 31, 11c, 5e, and 1—clearly indicates that the interglacials of MIS 31 (1081–1061 ka) and MIS 11c (422–394 ka) were warmer than those of MIS 5e (Last Interglacial) and MIS 1 (Holocene) [Melles et al. 2013]; Dark coniferous forest during MIS 11c was present instead of shrubland with birch and larch during MIS 5e and 1 forming the climax vegetation in the high arctic [Lozhkin & Anderson 2013].~~ 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, ~~these the latter~~ records do not show a prominent vegetation shift over the MBE.

For East Africa two terrestrial records and a marine one are available. From Lake Malawi, Johnson et al. [2016] infer wetter conditions and increased woodland vegetation between 800 and 400 ka based on the stable carbon isotopic composition of plant wax shifting from less to more strongly depleted values. Also from Lake Malawi, Ivory et al. [2018] published a pollen record of the past 600 ka revealing a number of phases of miombo woodland and mountain forest alternating with savannah vegetation (dry woodland and wooded grassland). Recently, a new record from Lake Magadi (Kenya) has been published indicating a change from wetter conditions to more aridity after 500 ka contrasting the Lake Malawi results [Owen et al. 2018]. In Lake Magadi, the representation of *Podocarpus* decreased over the MBE, while open grassy vegetation and salinity of the lake increased [Owen et al. 2018]. Neither the Lake Malawi nor the Lake Magadi records show dominant interglacial-glacial variability.

The marine record retrieved south of the Limpopo River mouth (Core MD96-2048) allows inferences about vegetation and climate in the catchment area of the Limpopo River draining large areas of South Africa, Botswana, Zimbabwe and Mozambique. Based on sediment chemistry, Caley et al. [2018] reported the effects of increased summer insolation in increased fluvial discharge and variability associated with eccentricity, which modulates precession amplitudes. Superimposed on the orbital-scale precipitation variability, a long-term trend from 1000 to 600 ka towards increased aridity in southeastern Africa was found [Caley et al. 2018]. The plant ~~leaf~~ wax carbon isotopic (hereafter $\delta^{13}\text{C}_{\text{wax}}$) record of the same core was originally interpreted as reflecting a trend toward increasingly drier glacial and wetter interglacials over the past 800 ka [Castañeda et al. 2016]. ~~Additionally, the average and relative~~ chain lengths of the plant leaf waxes exhibit a stepwise decrease at 430 ka suggesting a change from more shrub vegetation before the MBE to a larger contribution of trees during the post-MBE interglacials [Castañeda et al. 2016]. Thus, a pollen record of MD96-2048 has the potential to register the changes in interglacial vegetation cover over the

MBE. 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 which is expected to have had were more pronounced ~~effects~~ on the Southern Hemisphere [Yin & Berger 2010]. ~~However, t~~Until now, the palynology of only the last 350 ka has been published [Dupont et al. 2011] and, therefore, here we extend the pollen record of MD96-2048 to cover the past 800 ka in sufficient resolution. As described below, our new palynology results have led to the re-interpretation of the MD96-2048 $\delta^{13}\text{C}_{\text{wax}}$ record [Castañeda et al. 2016].

Previous work on Core MD96-2048

The sediments of MD96-2048 were retrieved in the middle of the Maputo Bight (Figure 1) from the southern Limpopo cone forming a depot center that has been build up at least since the Late Miocene [Martin 1981]. The site collects terrestrial material including pollen and spores mostly from the rivers ~~that~~ ~~discharge~~inge into the Maputo Bight of which the Limpopo River is the biggest draining large areas of northern South Africa and southern Mozambique. Apart from the so-called Bergwinds, the predominant wind direction is landward [Tyson & Preston-Whyte 2000] and aeolian input of terrestrial material is probably minor. Thus, pollen source areas would cover the region north of the Maputo Bight in southern Mozambique and the region west of Maputo of the Lebombo hills and the Drakensberg Escarpment [Dupont et al. 2011].

A wide variety of measurements have been performed on MD96-2048 sediments. Caley et al. [2011, 2018] recorded stable oxygen isotopes of benthic foraminifers (*Planulina wuellerstorfi*) providing a stable oxygen stratigraphy and age model aligned to the global stack LR04 [Lisiecki & Raymo 2005] for the past 2200 ka. Trace element (Mg/Ca ratios) of the planktic foraminifer *Globigernoides ruber sensu stricto* and foraminifer assemblages were combined to produce a robust sea surface temperature (SST) record [Caley et al., 2018]. High resolution (0.5 cm) XRF-scanning has been performed over the total core length, of which the iron-calcium ratios, $\ln(\text{Fe}/\text{Ca})$, were used to estimate fluvial terrestrial input variability [Caley et al., 2018]. At millennial resolution, higher plant leaf wax (*n*-alkane) concentrations and ratios and compound specific stable carbon isotopes ($\delta^{13}\text{C}_{\text{wax}}$) provided a record of vegetation changes in terms of open versus closed canopy and C4 versus C3 plants of the past 800 ka [Castañeda et al. 2016]. A very low resolution leaf wax deuterium isotopic record was generated [Caley et al. 2018], and in conjunction with other high-resolution proxies including $\ln(\text{Fe}/\text{Ca})$, was used to reconstruct rainfall and Limpopo River runoff during the past 2.0 Ma.

Present-day climate and vegetation

Modern climate is seasonal with the rainy season in summer (November to March). Yearly precipitation ranges from 600 mm in the lowlands to 1400 mm in the mountains, whereby rains are more frequent along the coast under the influence of SSTs [Jury et al. 1993, Reason & Mulenga 1999]. Annual average temperatures range from 24 to 16°C but in the highlands clear winter nights may be frosty.

The modern vegetation of this area belongs to the forest, Highveld grassland, and savannah biomes and also includes azonal vegetation (Figure 1) [Dupont et al. 2011 and references therein]. The natural potential vegetation of the coastal belt is forest, although at present it is almost gone; north of the Limpopo River mouth rain forests belong to the Inhambane phytogeographical mosaic and south of the Limpopo River the forest belongs to the Tongaland-Pondoland regional mosaic [White 1983]. The vegetation of the northern part of the Tongaland-Pondoland region is the Northern Coastal Forest [Mucina & Rutherford 2006]. Semi-deciduous forest is found in the Lebombo hills [Kersberg 1996]. Afromontane forest and Highveld grasslands grow along the escarpment and on the mountains. The savannahs of the Zambezi phytogeographical region including e.g. the miombo dry

forest occur further inland [White 1983]. Azonal vegetation consists of freshwater swamps, alluvial, and seashore vegetation and mangroves [Mucina & Rutherford 2006].

Material and Methods

Pollen analysis of the 37.59 m long core MD96-2048 (26°10'S 34°01'E, 660m water depth) was extended with 65 samples down core to 12 m (790 ka). Average sampling distance for the Brunhes part was 7 cm reaching an average temporal resolution of 4 ka according to the age model based on the stable oxygen isotope stratigraphy of benthic foraminifers [Caley et al. 2011, 2018]. Two older windows have been sampled; 20 samples between 15 and 26 m (943-1537 ka) and 19 samples between 30 and 36 m (1785-2143 ka) were taken with an average resolution of 31 and 20 ka, respectively.

Pollen preparation has been described in [Dupont et al. 2011]. In summary, samples were decalcified with HCl (~10%), treated with HF (~40%) for two days, ultrasonically sieved over an 8- μ m screen and, if necessary, decanted. The samples were spiked with two *Lycopodium* spore tablets (either of batch #938934 or batch #177745). Residues were mounted in glycerol and pollen and spores examined at 400x or 1000x magnification. Percentages are expressed based on the total of pollen and spores ranging from over 400 to 60 – only in six samples this sum amounts to less than 100. Confidence intervals (95%) were calculated after Maher [1972, 1981]. Pollen have been identified using the reference collection of African pollen grains of the Department of Palynology and Climate Dynamics

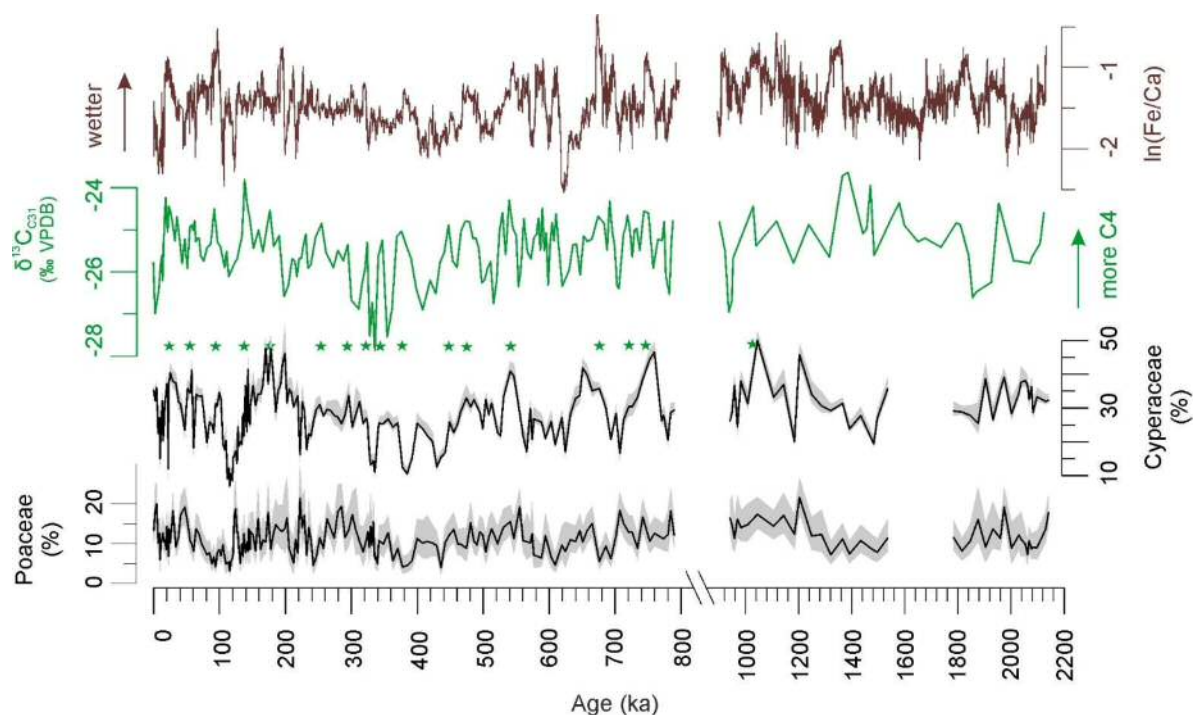


Figure 2. Indicators of C4 vegetation and terrestrial input. From top to bottom: elemental Fe/Ca ratios [Caley et al. 2018]; less negative values indicate relatively wetter conditions, $\delta^{13}\text{C}_{\text{wax}}$ of the *n*-alkane C_{31} [Castañeda et al. 2016, Caley et al. 2018]; less negative values of around -24‰ indicate more C4 inputs while more negative values of around -28‰ indicate more C3 inputs, Cyperaceae (sedges) pollen percentages [Dupont et al., 2011, this study], Poaceae (grass) pollen percentages [Dupont et al., 2011, this study]. Shaded areas denote 95% confidence intervals after [Maher 1972]. Stars denote corresponding maxima in Cyperaceae pollen percentages and the stable carbon isotopes indicating C4 vegetation. VPDB: Vienna Pee Dee Belemnite. [Note the scale break.](#)

of the University of Göttingen, the African Pollen Database collection, and literature [e.g. Bonnefille & Riollet 1980, Scott 1982, Köhler & Brückner 1982, 1989, Schüler & Hemp 2016].

We assigned pollen taxa to groups such as riparian, woodland, forest, etc. (Supplementary Table 1) using information given by Scott [1982], White [1983], Beentje [1994], Kersberg [1996], Coates-Palgrave [2002], Vincens et al. [2007]. 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. ~~using a version of the unmixer algorithm programmed in MATLAB by Dave Heslop in 2008.~~ 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. We use a version of the unmixer algorithm programmed in MATLAB by Dave Heslop in 2008. Taxa occurring in 6 or more samples (listed in Supplementary Table 2) were used in the endmember modelling (148 of 231 taxa in 220 samples). We selected a model with four components explaining ~~over more than~~ 95% of the variance ($r^2 = 0.953$). Iteration was stopped at 1000x resulting in a convexity at termination of -1.6881. Significance level at 99% for taxa to score on the assemblages was 0.018.

To study the correlations between different parameters, we used a linear regression model (least square regression) on linearly interpolated values (5 ka steps) from 0 to 790 ka. Correlation coefficients are given in Table 1. For interpolation and testing the correlation, we used the package PAST [Hammer et al. 2001].

Result and Discussion

Terrestrial input and provenance of the C4 plant wax

Pollen percentages of Cyperaceae (sedges) and Poaceae (grasses) are plotted in Figure 2 together with the $\delta^{13}\text{C}_{\text{wax}}$ of the ~~n-alkane~~ C_{31} ~~n-alkane~~ and XRF-scanning data. ~~($\ln(\text{Fe}/\text{Ca})$, the natural logarithm of elemental ratios of iron over calcium).~~ Comparing the records of Cyperaceae and $\delta^{13}\text{C}_{\text{wax}}$ reveals that high relative amounts of C4 plant material co-varied with increased representation of sedges. They also co-varied with higher terrestrial input indicated by $\ln(\text{Fe}/\text{Ca})$, and increased precipitation as suggested by deuterium of the C_{31} n-alkane [Caley et al., 2018]. We substantiated the correlations for the Brunhes Chron between pollen percentages, leaf waxes and elemental ratios in Table 1. Leaf wax data are after Castañeda et al. [2016] including Average Chain Length (ACL) of the C_{27} - C_{33} n-alkanes, the ratio of $\text{C}_{31}/(\text{C}_{31}+\text{C}_{29})$ and $\delta^{13}\text{C}_{\text{wax}}$ ~~and~~ ~~XRF~~ $\ln(\text{Fe}/\text{Ca})$ ratios ~~are~~ from Caley et al. [2018]. Significant correlation is found between the leaf wax parameters and Cyperaceae data but not between $\delta^{13}\text{C}_{\text{wax}}$

Table 1. Correlation coefficients calculated with PAST [Hammer et al 2001]. Significant correlations are underlined (95%) or bold and underlined (99%). Average Chain Length (ACL), ratio of concentrations of $\text{C}_{31}/(\text{C}_{31} + \text{C}_{29})$, and stable carbon isotope composition of the C_{31} n-alkane ($\delta^{13}\text{C}_{\text{wax}}$) after Castañeda et al. [2016]. Cyperaceae and Poaceae pollen percentages (of total pollen and spores) after Dupont et al. [2011] and this study. $\ln(\text{Fe}/\text{Ca})$ data after Caley et al. [2018].

		Ratio	$\delta^{13}\text{C}_{\text{wax}}$	Cyperaceae	Poaceae	XRF
r^2	ACL	$\text{C}_{31}/(\text{C}_{29}+\text{C}_{31})$	(‰)	(%)	(%)	$\ln(\text{Fe}/\text{Ca})$
ACL	1					
Ratio $\text{C}_{31}/(\text{C}_{31}+\text{C}_{29})$	<u>0.635</u>	1				
$\delta^{13}\text{C}_{\text{wax}}$	<u>0.079</u>	<u>0.180</u>	1			
Cyperaceae (%)	0.027	<u>0.140</u>	<u>0.142</u>	1		
Poaceae (%)	0.003	0.016	0.003	<u>0.165</u>	1	
XRF $\ln(\text{Fe}/\text{Ca})$	0.016	<u>0.032</u>	<u>0.227</u>	<u>0.110</u>	0.011	1

(indicative of C4 inputs) and Poaceae pollen percentages - although a correlation exists between Cyperaceae and Poaceae percentages. While the sedge pollen percentages fluctuate between 10 and 50% (mostly > 20%), the percentages of grass pollen are always lower than 20%. Such low grass pollen values have not been found adjacent C4 grass dominated biomes (mainly savannahs) on the western side of the continent [Dupont 2011]. It is, therefore, likely that in sediments of MD96-2048 the C4 component of the plant wax originated ~~mainly~~ from C4 sedges rather than from C4 grasses.

South Africa has 68 species of Cyperaceae (sedges) of which 28 use the -C4 sedges pathway (among the 10 *Cyperus* species 8 are C4) predominantly growing in the northern part of the country - of which papyrus is the most well-known [Stock et al. 2004]. They are an important constituent of tropical swamps and riversides [Chapman et al. 2001]. An inventory of six modern wetlands between 500 and 1900m in KwaZulu Natal shows that C4 grasses dominate the dry surroundings of the wetlands at all altitudes [Kotze & O'Connor 2000]. In the wet parts of the wetlands, however, C4 sedges may make up to 60% of the vegetation cover at 550 m. At higher altitudes the coverage of C4 sedges declines [Kotze & O'Connor 2000].

~~Furthermore~~ Cyperaceae pollen concentration (Figure 3) and percentages correlated with $\ln(\text{Fe}/\text{Ca})$ and ~~the latter~~ with $\delta^{13}\text{C}_{\text{wax}}$ (Table 1, Figure 2). The ratios of terrestrial iron over marine calcium can be interpreted as a measure for terrestrial input, which in this part of the ocean is mainly fluvial. Correlation between increased fluvial discharge and increased C4 vegetation as well as increased Cyperaceae pollen has been reported from sediments off the Zambezi [Schefuß et al. 2011, Dupont & Kuhlmann 2017]. Moreover, a fingerprint of C4 sedges was found in Lake Tanganyika [Ivory & Russel 2016]. As a consequence, material (leaf waxes and pollen) from the riverine vegetation is probably better represented than that from dry and upland vegetation. These results corroborate the reinterpretation of the $\delta^{13}\text{C}_{\text{wax}}$ record, in which the increased representation of C4 plants (*n*-alkanes enriched in ^{13}C) is instead attributed to stronger transport of material from the upper Limpopo catchment and the extension of swamps containing C4 sedges under more humid conditions [Caley et al., 2018]. Previously Castañeda et al. [2016] had interpreted increased C4 inputs as reflecting increased aridity.

Relatively low values of Cyperaceae pollen and Fe/Ca ratios are found for most interglacials of the Brunhes Chron (Figures 2 and 3), which could be interpreted as an effect of sea-level high-stands. However, Caley et al. [2018] demonstrated that the fluvial discharge is not related to sea-level changes. From the bathymetry of Maputo Bay, strong influence of sea-level is also not expected because the shelf is not broad and the locality of Core MD96-2048 is relatively remote on the Limpopo cone in the center of the clockwise flowing Maputo Bight Lee Eddy. The eddy transports terrestrial material northeastwards before it is taken southwards (Figure 1) [Martin 1981] and likely has not changed direction during glacial times. Thus, fluvial discharge was probably low during interglacials (among other periods), which might be the combined result of more evapotranspiration and less precipitation. ~~It is remarkable that despite the drier conditions,~~ the representation of woodland and dry forest is relatively high during the interglacial periods (Figure 3, see also next section).

Endmembers representing vegetation on land

Palynological results have been published for the past 350 ka [Dupont et al. 2011] providing a detailed vegetation record for the past three climate cycles. Pollen and spore assemblages could be characterized initially by three ~~so-called~~ endmembers via endmember modelling (EM1, EM2, EM3). The assemblage of EM1 was dominated by *Podocarpus* (yellow wood) pollen percentages being more abundant during the non-interglacial parts of MIS 5, 7, and 9. EM2 was characterized by pollen percentages of Cyperaceae (sedges), Ericaceae (heather) and other plants of open vegetation and

abundant during full glacial stages. EM3 constituted of pollen from woodland, forest, and coastal vegetation and was interpreted to represent a mix of several vegetation complexes.

We repeated the endmember modelling for the extended record covering the entire Brunhes Chron and the two early Pleistocene windows. With the extended dataset, cumulative increase of explanatory power lessened after four (instead of three) endmembers. Therefore, a model with four endmembers was chosen. We used the scores of the different pollen taxa on the endmember assemblages for our interpretation of the endmembers (list of taxa and scores in Supplementary Tables 1 and 2). We compare the new results with the previous analysis. ~~Although To distinguish~~ between the previous and current analysis (which show strong similarities), we have given new names to the endmember assemblages reflecting our interpretation. A selection of pollen percentage curves are plotted together with each endmember's fractional abundance in Supplementary Figures 1-4.

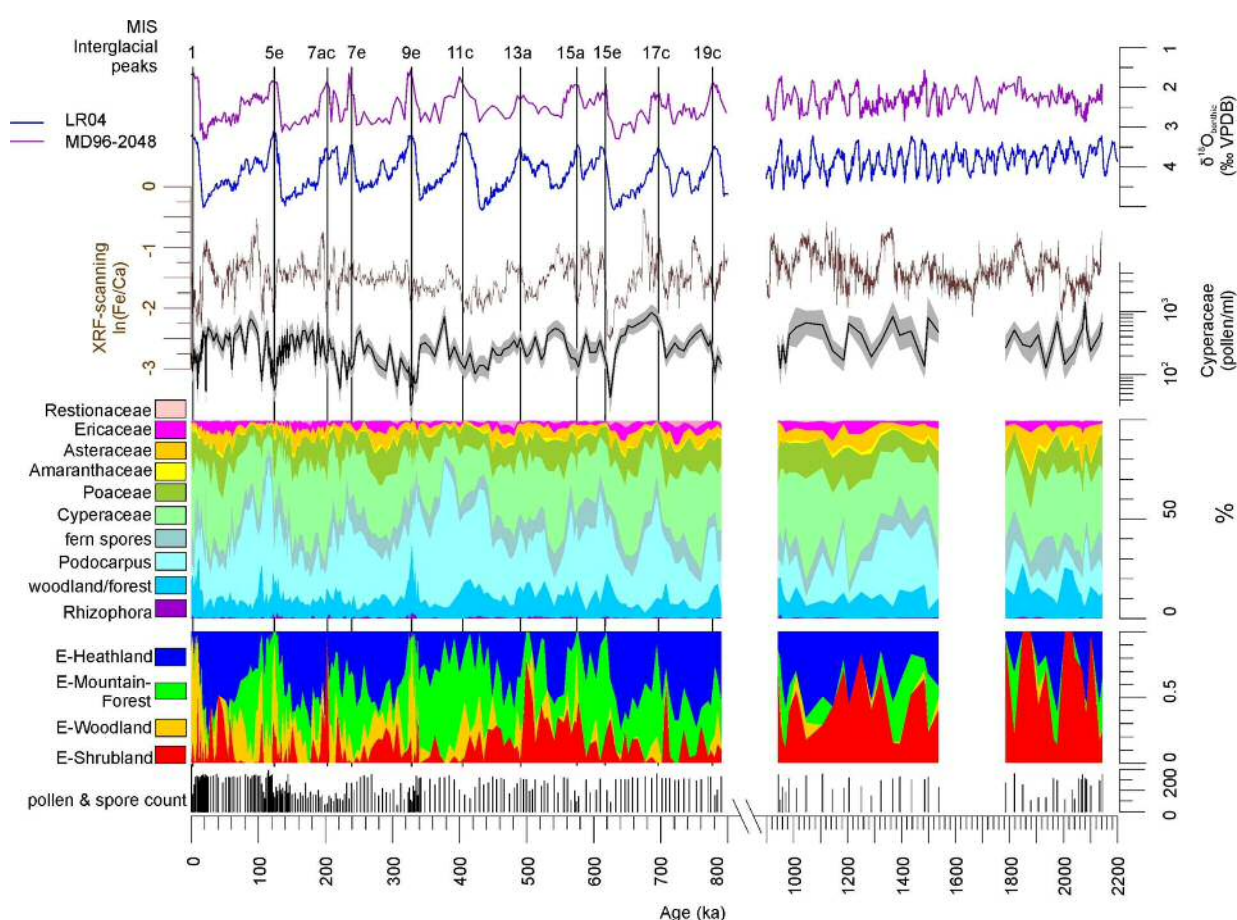


Figure 3. Summary of results of MD96-2048. Bottom to top: Pollen and spore count used to calculate percentages; Fractional abundance of endmembers E-Shrubland, E-Woodland, E-Mountain-Forest, and E-Heathland; Pollen summary diagram (woodland and forest taxa are listed in Supplementary Table 1; Cyperaceae pollen concentration per ml (shading denoted 95% confidence intervals after Maher [1981]; ln(Fe/Ca); global stack of stable oxygen isotopes of benthic foraminifers, LR04 [Liesiecki & Raymo 2005]; $\delta^{18}\text{O}_{\text{benthic}}$ of Core MD96-2048 [Caley et al. 2018]; Interglacial peaks after PAGES [2016]. VPDB: Vienna Pee Dee Belemnite.

Of the now four endmember assemblages (Figure 3), ~~one endmember had a counterpart in one~~ endmember has almost the same composition as EM2 [Dupont et al. 2011] of the previous analysis. Not only composition but also the fractional abundances, which were high during glacial stages, are very much alike. We name this endmember 'E-Heathland', which is dominated by Cyperaceae

(sedges) pollen percentages followed by Ericaceae (heather) [pollen](#) and hornwort (Anthocerotaceae) spores. Also *Lycopodium* (clubmoss) spore, Restionaceae and *Stoebe*-type pollen percentages score highest on this endmember. The E-Heathland assemblage represents a Fynbos-like open vegetation growing during full glacials. Other pollen records from SE Africa also indicate an open ericaceous vegetation with sedges and Restionaceae during glacial times [Scott 1999, Dupont & Kuhlmann 2017]. The record of MD96-2048 testifies that this type of open glacial vegetation regularly occurred since at least two million years.

Like the endmember EM1 [Dupont et al. 2011] of the previous analysis, one endmember is dominated by *Podocarpus* (yellow wood) pollen percentages. The assemblage is enriched by pollen of *Celtis* (hackberries) and *Olea* (olive trees) accompanied by undifferentiated fern spores. The interpretation as an assemblage representing mountain forest is rather straightforward and we name the assemblage 'E-Mountain-Forest'. 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 pCO₂ are particularly low](#) (Figure 3). It is low in the early [Pliocene–Pleistocene](#) parts of the record.

The remaining endmember assemblages have no direct counterpart in the previous analysis, although summed together the pattern of fractional abundance is similar to that of EM3 [Dupont et al. 2011]. One endmember groups together 44 pollen taxa, mostly from coastal and dune vegetation, which we name 'E-Shrubland'. It includes pollen of Asteraceae and Poaceae (grasses). The latter are not very specific as grass pollen values score almost as high on other endmember assemblages (E-Heathland and E-[ShrublandWoodland](#)). Several taxa scoring on this endmember are known from coastal or halophytic settings such as *Gazania*-type, Amaranthaceae, *Tribulus*, Acanthaceae and *Euphorbia*-type. Arboreal taxa in this assemblage are *Dombeya*, *Acacia*, Meliaceae/Sapotaceae. The most typical taxa are the *Buxus* species. We distinguished three types of *Buxus* pollen: *B. macowani* type, *B. hildebrandtii* [type](#) and *B. cf. madagascariensis* [Köhler & Brückner 1982, 1989]. *B. madagascariensis* grows on Madagascar and [its pollen is only found sporadically, while](#) the other two species inhabit bushland and forest on coastal dunes of the East African main-land. *B. hildebrandtii* nowadays is found in Somalia and Ethiopia and *B. macowani* is native in South Africa. The record of MD96-2048 indicates that these *Buxus* species were more common in the early Pleistocene than during the Brunhes Chron ([Figure 3](#)).

The last endmember, which we name 'E-Woodland', groups together 39 pollen taxa from forest and woodland species with maximum values of less than 5 or 2% of the total of pollen and spores. To this assemblage belong *Pseudolachnostylis*, *Dodonaea viscosa* and *Manilkara*, which are woodland trees. *Protea* (sugarbush) and *Myrsine africana* (Cape myrtle) grow more upland and *Alchornea* is a pioneer forest tree often growing along rivers. Others include wide-range woodland taxa [such as Combretaceae species](#). The occurrence of pollen of *Brachystegia* (miombo tree), *Burkea africana*, *Spirostachys africana* and *Hymenocardia* in this assemblage is indicative of Miombo dry forest and woodland. The assemblage additionally includes Rhizophoraceae pollen from the coastal mangrove forest. The fractional abundance of the E-Woodland assemblage is low during the early Pleistocene, increased during the interglacials prior to the MBE and had maximum values during Interglacials 9e, 5e, and 1 ([Figures 3, 4](#)). These interglacials also exhibited maximum percentages of arboreal pollen excluding *Podocarpus*.

In summary, the endmember analysis indicates a very stable open ericaceous vegetation with partially wet elements such as sedges and Restionaceae characterizing the landscape of full glacials ([when global temperatures and pCO₂ were lowest](#)). During the less extreme parts of the glacials, mountain *Podocarpus* forest was extensive as in most mountains of Africa [Dupont 2011, Ivory et al. 2018]. On the other hand, interglacials were characterized by coastal shrubs. In the course of the

Brunhes, the woody component, which was relatively weak before the MBE, became more and more important reflecting the same long-term trend found in the leaf wax records [Castañeda et al. 2016]. It is likely that the Miombo dry forest and woodland ~~developed-migrated into~~ the region in the ~~course-successive interglacials~~ of the Brunhes Chron. Particularly during Interglacials 9e and 1 the area might have been more forested than during the older interglacials of the Brunhes Chron.

Long-term trends in vegetation and climate of East Africa

The region of the Limpopo River becoming more and more wooded in the course of successive interglacials [Castañeda et al. 2016] somewhat paralleled the conditions around Lake Malawi [Johnson et al. 2016]. However, around Lake Malawi, forested phases of either mountain forest, seasonal forest, or Miombo woodland alternating with savannahs occurred during both glacial and interglacial stages [Ivory et al. 2018]. Also in contrast to the Lake Malawi record, the MD96-2048 Poaceae pollen percentages fluctuated little and remained relatively low (less than 20%) indicating that savannahs were of less importance in the Limpopo catchment area and the coastal region of southern Mozambique.

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]. Antiphase behavior of SE African climate with that of West and East Africa emphasizes the importance of the average position of the tropical rainbelt shifting southwards during globally cold periods as has been inferred from Holocene to Last Glacial records of Lake Malawi [Johnson et al. 2002, Scholz et al. 2011]. Our results confirm this relationship existed over the entire Brunhes Chron.

The Lake Malawi pollen record as well as that of the equatorial Lake Magadi in Kenya [Owen et al. 2018] do not show much of a glacial-interglacial rhythm and are dominated by the precession variability in tropical rainfall [cf. Clement et al. 2004]. Obviously, in the tropical climate of the Southern Hemisphere north of ~15°S the hydrological regime had more effect on the vegetation than changes in temperature, while further south the impact of glacial-interglacial variability on the vegetation increased.

Effects of atmospheric $p\text{CO}_2$

While the hydroclimate of the region shows precession variability [Caley et al. 2018], the vegetation ~~is more affected by the~~ shows a glacial-interglacial ~~pattern-rhythm~~ (Supplementary Information) indicating that besides hydrology, temperature and/or atmospheric $p\text{CO}_2$ levels were important drivers of the vegetation development. Combining the results of the pollen assemblages with stable carbon isotopes and element~~al~~ information indicates that during interglacials the region of SE Africa (northern South Africa, Zimbabwe, southern Mozambique) was less humid. This is in accordance ~~to~~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 $p\text{CO}_2$ levels during the post-MBE interglacials might have favored tree growth ~~as higher $p\text{CO}_2$ 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 $p\text{CO}_2$ are high, the mountain forest is replaced by woodland (Figure 4). It might be only after interglacial $p\text{CO}_2$ 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 $p\text{CO}_2$ exceeding ~ 220 ppmv (Figure 5). This holds also for the Interglacials 19c, 17c, 15e, 15a, 13a, and 7e, in which $p\text{CO}_2$ 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 $p\text{CO}_2$ dropped below ~ 220 ppmv during those colder

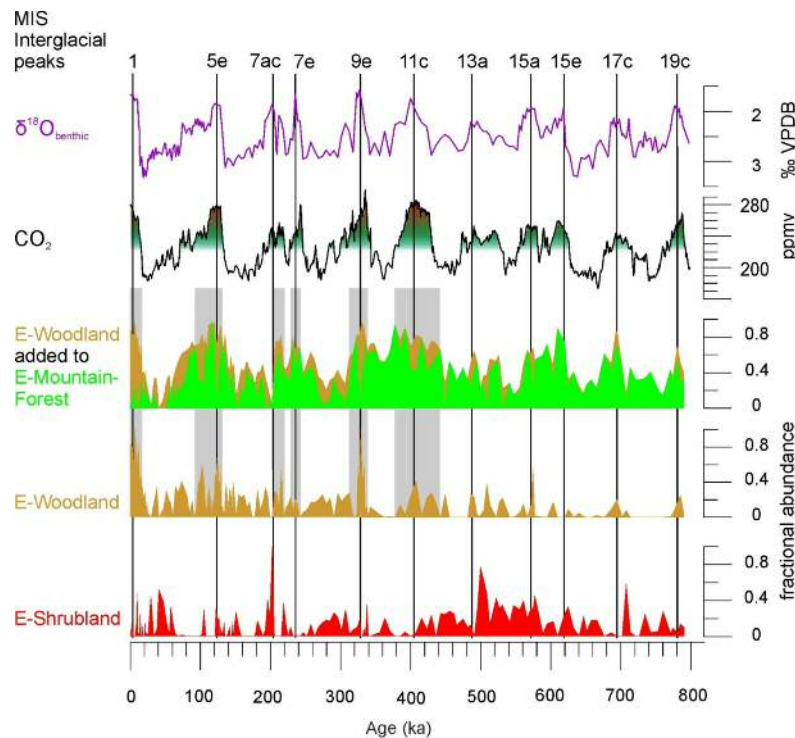


Figure 4: Comparing pollen assemblages E-Mountain-Forest, E-Woodland and E-Shrubland with atmospheric CO_2 [Bereiter et al. 2015, PAGES 2016, Barnola et al. 1987, Siegenthaler et al. 2005, Lüthi et al. 2008]. On top Interglacial peaks of the past 800 ka [PAGES 2016] and stable oxygen isotopes of benthic foraminifera ($\delta^{18}\text{O}_{\text{benthic}}$) 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.

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 $p\text{CO}_2$ 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 ($1\text{--}3^\circ\text{C}$ lower temperatures, less precipitation, 200 ppmv $p\text{CO}_2$) depended hardly on temperature but primarily on increased aridity and somewhat on lower $p\text{CO}_2$, whereby lower $p\text{CO}_2$ 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 in the East and Southeast African Mountains might well be the result of low when atmospheric $p\text{CO}_2$ in combination with low and temperatures were low.

1 However, low temperatures are not particularly favorable for C4 sedges as indicated by the
2 altitudinal distribution of C4 sedges in modern wetlands of KwaZulu Natal [Kotze & O'Connor 2000]
3 [Jolly & Haxeltine 1997]. We presume, therefore, that the extension of C4 sedges during the more
4 humid phases of the glacials is the result of low atmospheric CO₂ concentrations rather than of low
5 temperatures.

6 Pollen records of ericaceous vegetation suggest an extensive open vegetation existing in the East
7 African Mountains [e.g. Coetzee 1967, Bonnefille & Rioulet 1988, Marchant et al. 1997, Debussk 1998,
8 Bonnefille & Chalié 2000] and in SE Africa and Madagascar [e.g. Botha et al. 1992, Scott 1999, Gasse
9 and Van Campo 2001, Scott & Tackeray 1987] during the last glacial. In our study, ericaceous fynbos-
10 like vegetation (E-Heathland) was found for those parts of the glacials having lower (less than ~220
11 ppmv) atmospheric pCO₂ (Figure 5). Exceptions were found for MIS 12 and 14 when the difference of
12 pCO₂ with that of the preceding stage was small [Bereiter et al. 2015]. Dupont et al. [2011] argued
13 that increase of C4 vegetation as the result of low pCO₂ was unlikely because no extension of grasses
14 was recorded. However, this argument is flawed if sedges dominantly constituted the C4 vegetation
15 in the area. We also note that in many parts of South Africa, no substantial increase of C4 grasses
16 occurred but that many sites suggest an expansion of C3 grasses during the Last Glacial Maximum
17 [Scott 2002].

18 ~~Pollen records of mountain sites on both sides of the Congo basin showed some influence of CO₂~~
19 ~~concentrations, which influence varied in the different environments [Izumi & Lézine 2016].~~
20 ~~Moreover, the record of mountain forest in SE Africa indicates some extension of moist *Podocarpus*~~
21 ~~forest during those parts of the glacial stages with atmospheric pCO₂ exceeding ~220 ppmv (Figure~~
22 ~~5). This holds also for the Interglacials 19c, 17c, 15e, 15a, 13a, and 7e, in which not only pCO₂ but also~~
23 ~~Antarctic temperatures were subdued. A picture emerges of cool glacial stages in SE Africa in which~~
24 ~~tree cover broke down when atmospheric pCO₂ became too low. During Interglacials 11c, 9e, 7ac, 5e,~~
25 ~~and 1 the mountain forest is replaced by woodland (Figure 4). A picture emerges of cool glacial~~
26 ~~stages in SE Africa in which tree cover broke down when atmospheric pCO₂ became too low. It might~~
27 ~~be only after interglacial pCO₂ levels rose over ~250 ppmv that Miombo woodland could establish in~~
28 ~~the area further extending during the warm and relatively dry post-MBE interglacials.~~

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

Pollen records of ericaceous vegetation suggest an extensive open vegetation existing in the East African Mountains [e.g. Coetzee 1967, Bonnefille & Rioulet 1988, Marchant et al. 1997, Debussk 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-Heather) was found for those parts of the glacials having lower (less than ~230 ppmv) atmospheric $p\text{CO}_2$ (Figure 5). Exceptions were found for MIS 12 and 14 when the difference of $p\text{CO}_2$ with that of the preceding stage was small [Barnola et al. 1987, Siegenthaler et al. 2005, Lüthi et al. 2008]. Dupont et al. [2011] argued that increase of C4 vegetation as the result of low $p\text{CO}_2$ was unlikely because no extension of grasses was recorded. However, this argument is flawed if sedges dominantly constituted the C4 vegetation in the area.

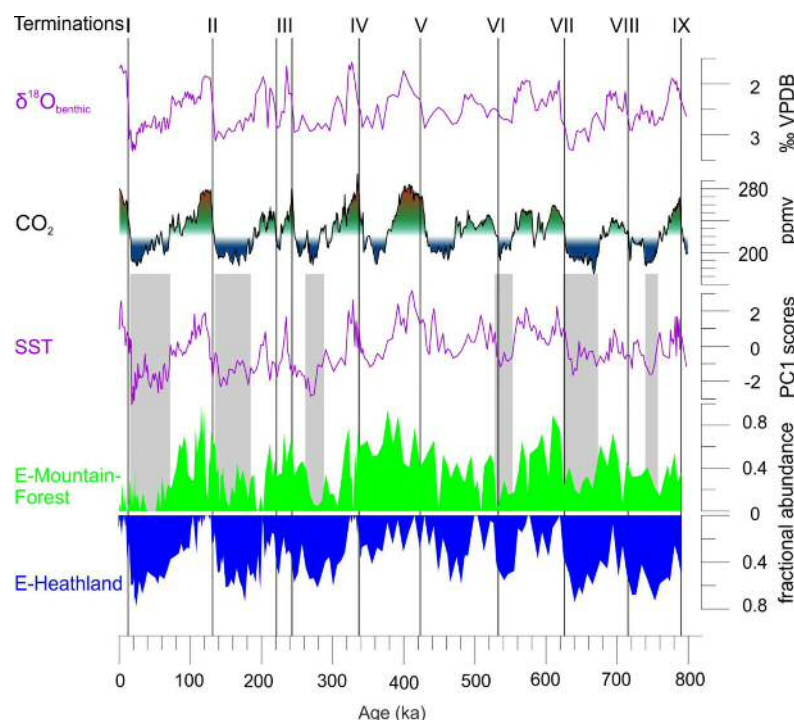


Figure 5: Comparing glacial pollen assemblages E-Mountain-Forest and E-Heatherland with atmospheric CO_2 [Barnola et al. 1987, Siegenthaler et al. 2005, Lüthi et al. 2008, Bereiter et al. 2015, PAGES 2016] and sea surface temperatures of the southeastern Indian Ocean (SST PC1 scores of MD96-20468) [Caley et al. 2018]. On top Terminations of the past 9 glaciations and stable oxygen isotopes of benthic foraminifera ($\delta^{18}\text{O}_{\text{benthic}}$) 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.

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 ~~is 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]. ~~Still, the C4/C3 sedge ratios in those wetlands decline with altitude and temperature. 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.~~

~~Long term trends in vegetation and climate of East Africa~~

~~The region of the Limpopo River becoming more and more wooded in the course of successive interglacials [Castañeda et al. 2016] somewhat paralleled the conditions around Lake Malawi [Johnson et al. 2016]. However, around Lake Malawi, forested phases of either mountain forest, seasonal forest, or Miombo woodland alternating with savannahs occurred during both glacial and interglacial stages [Ivory et al. 2018]. Also in contrast to the Lake Malawi record, the MD96-2048 Poaceae pollen percentages fluctuated little and remained relatively low indicating that savannahs were of less importance in the Limpopo catchment area and the coastal region of southern Mozambique.~~

~~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 development around the equator (and in the Northern Hemisphere). At the equator a trend to less forest around Lake Magadi marks the Mid-Brunhes transition [Owen et al. 2018]. Antiphase behavior of SE African climate with that of West and East Africa emphasizes the importance of the average position of the tropical rainbelt shifting southwards during globally cold periods as has been inferred from Holocene to Last Glacial records of Lake Malawi [Johnson et al. 2002, Scholz et al. 2011]. Our results confirms this relationship existed over the entire Brunhes Chron.~~

~~The Lake Malawi pollen record as well as that of the equatorial Lake Magadi in Kenya [Owen et al. 2018] do not show much of a glacial-interglacial rhythm and are dominated by the precession variability in tropical rainfall [cf. Clement et al. 2004]. Obviously, in the tropical climate of the Southern Hemisphere north of ~15°S the hydrological regime had more effect on the vegetation than changes in temperature, while further south the impact of temperature on the vegetation increased.~~

Conclusions

Palynology in combination with sediment chemistry and carbon isotope analysis of leaf waxes carried out on the marine sediments of MD96-2048 retrieved from the Limpopo River cone in the Maputo Bay (SE Africa) allowed a detailed reconstruction of the ~~vegetation biome~~ developments over the Brunhes Chron and comparison with earlier Pleistocene vegetation of SE Africa.

Using endmember modelling, we could distinguish four pollen assemblages: E-Heathland, E-Mountain-Forest, E-Shrubland, E-Woodland. The open sedge-~~ridge~~ and ericaceous vegetation represented by E-Heathland occurred during those parts of the glacials with lower temperatures and atmospheric $p\text{CO}_2$. *Podocarpus*-rich mountain forest represented by E-Mountain-Forest extended during the less extrem parts of the glacials. E-Shrubland represents a shrublike vegetation with coastal elements and *Buxus* species and mainly occurred during the earlier Pleistocene (before 1 Ma). E-Woodland represents interglacial woodlands, Miombo woodland in particular, becoming more and more important in the successive interglacial stages of the Brunhes Chron and dominated the post-MBE interglacials.

Our results indicate ~~the strong~~ influence of atmospheric $p\text{CO}_2$ fluctuations on the shaping of the biomes in SE Africa during the Brunhes Chron. ~~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 $p\text{CO}_2$. (2) Because of the correlation between Cyperaceae pollen percentages and $\delta^{13}\text{C}_{\text{wax}}$ and the lack of correlation between Poaceae percentages and $\delta^{13}\text{C}_{\text{wax}}$ in combination with the relatively low grass pollen percentages, we deduce that the C4 plant imprint mainly derives from the sedges. (3) The extensionexpansion? of C4 sedges during the colder periods of the glacials is unlikely theto result from-of lower temperatures. Thus, Dduring the colder phases of~~

the glacials, low atmospheric $p\text{CO}_2$ might have favored the ~~extension~~ expansion of C4 sedges. (4) The confinement of mountain forest to the glacial periods with moderate temperatures and moderate $p\text{CO}_2$, and the lack of extension into the lowlands of mountain forest during the colder periods, suggests that low $p\text{CO}_2$ became restrictive to the forest. Mountain forests could thrive during glacials as long as $p\text{CO}_2$ levels exceeded ~ 220 ppmv. (5) Based on the elemental composition as a proxy for river discharge [$\ln(\text{Fe}/\text{Ca})$], we estimate the post-MBE interglacials as the drier intervals of the sequence. Nevertheless woodland extended during those periods, which we attribute to increased temperatures and $p\text{CO}_2$. Atmospheric $p\text{CO}_2$ levels over 250 ppmv might have been a prerequisite for the establishment of the Miombo woodlands in SE Africa, which extended during the post MBE interglacials.

The vegetation record of the Limpopo catchment area ~~showed more~~ shows a greater impact of glacial-interglacial variability, mainly driven by CO_2 fluctuations, and less ~~effects-influence of the~~ hydroclimate compared to the more equatorial records of Lake Malawi and Lake Magadi. The long-term trend of increased woodiness in the course of the Brunhes Chron paralleled that of Lake Malawi but contrasted Lake Magadi suggesting a long-term southward shift in the average position of the tropical rainbelt.

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Data availability

Pollen counts are available at <https://doi.pangaea.de/10.1594/PANGAEA.897922>.

Previously published data can be retrieved at <https://doi.pangaea.de/10.1594/PANGAEA.895364>;
<https://doi.pangaea.de/10.1594/PANGAEA.895361>;
<https://doi.pangaea.de/10.1594/PANGAEA.895362>;
<https://doi.pangaea.de/10.1594/PANGAEA.863919>;
<https://doi.pangaea.de/10.1594/PANGAEA.895357>.

Author contributions

LMD carried out the palynological analysis, conceived and wrote the manuscript, TC carried out the sedimentology and stratigraphy and contributed to the discussion, ISC conducted the stable isotope analysis on plant waxes and contributed to the discussion.

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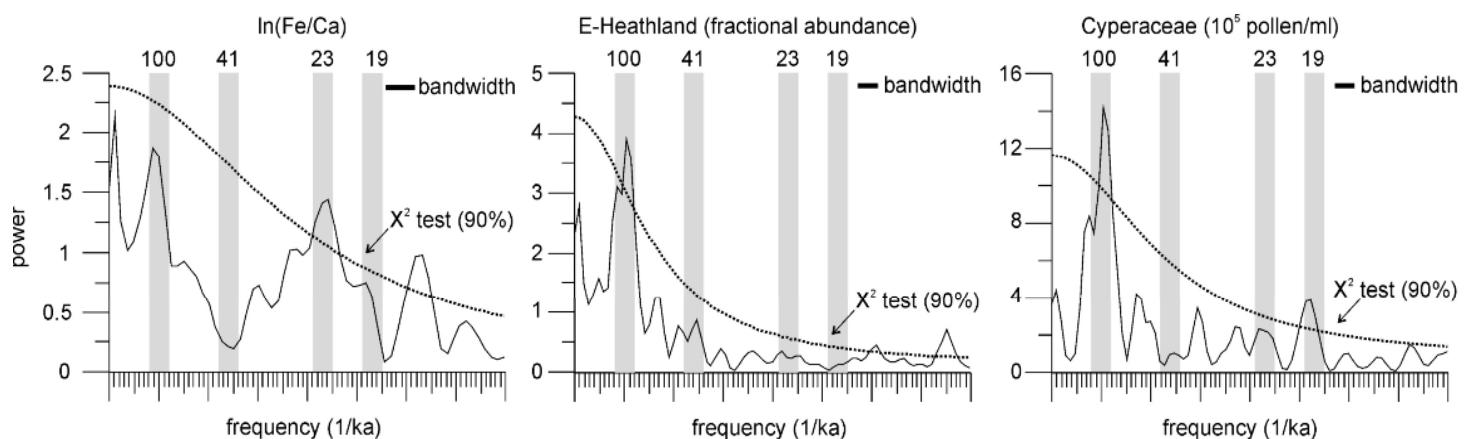
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Supplement

contains

REDFIT frequency analysis

We conducted a frequency analysis on the data of the $\ln(\text{Fe}/\text{Ca})$ 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 $\ln(\text{Fe}/\text{Ca})$ 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 $\ln(\text{Fe}/\text{Ca})$ 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 χ^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 $\ln(\text{Fe}/\text{Ca})$ 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.



Supplementary References

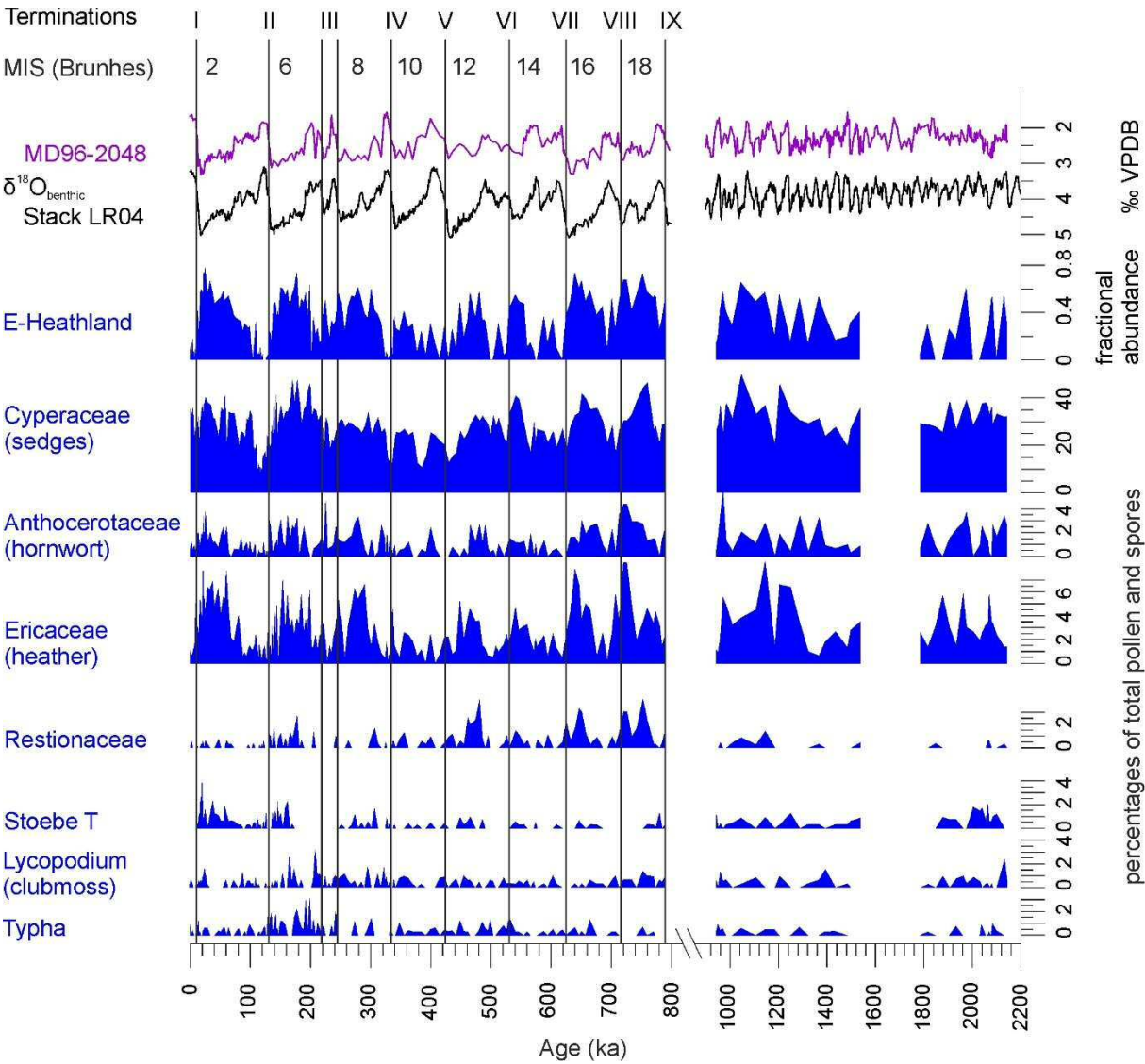
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Excel-Tables

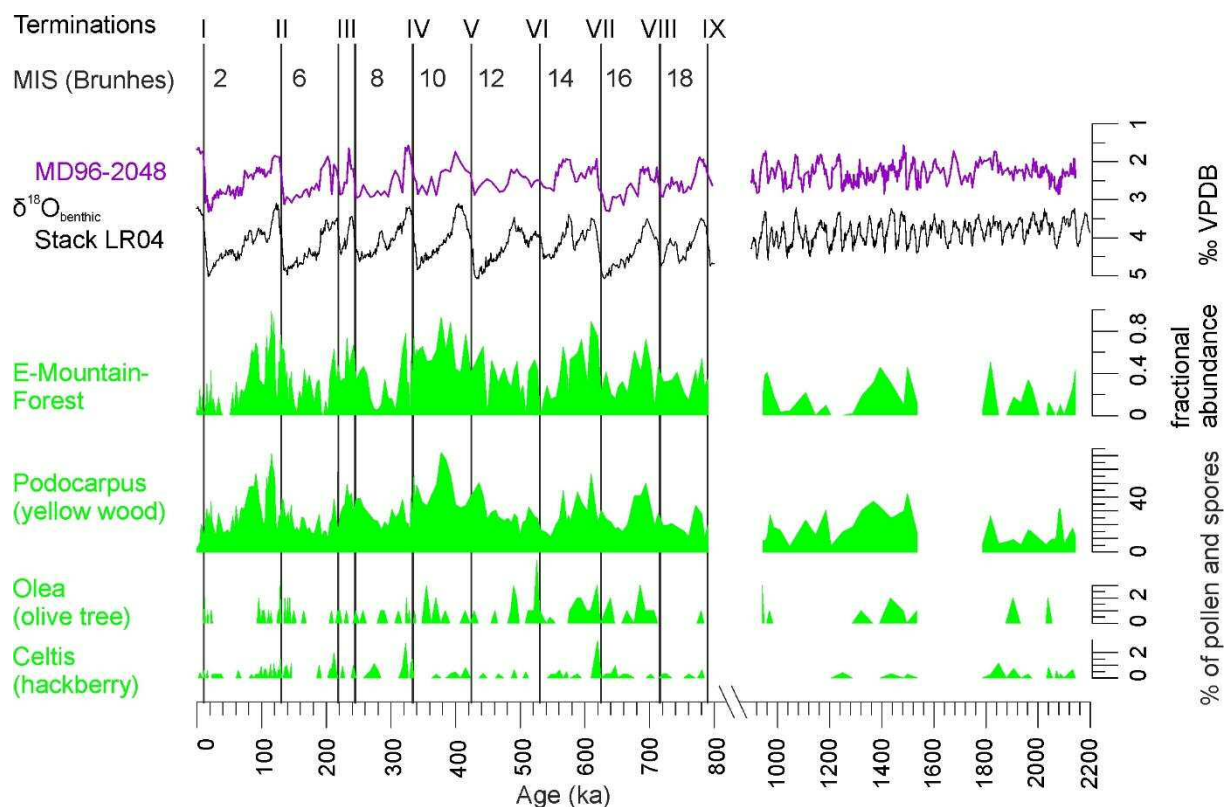
Supplementary Table 1: Family, Pollen taxon, group, growth form, endmember assemblage of maximum score.

Supplementary Table 2: Family, Pollen taxon, group, growth form, score per endmember (E-Mountain-Forest, E-Heathland, E-Woodland, E-Shrubland), significance of taxon scores (r^2) for two endmember analyses [this study and Dupont et al. 2011].

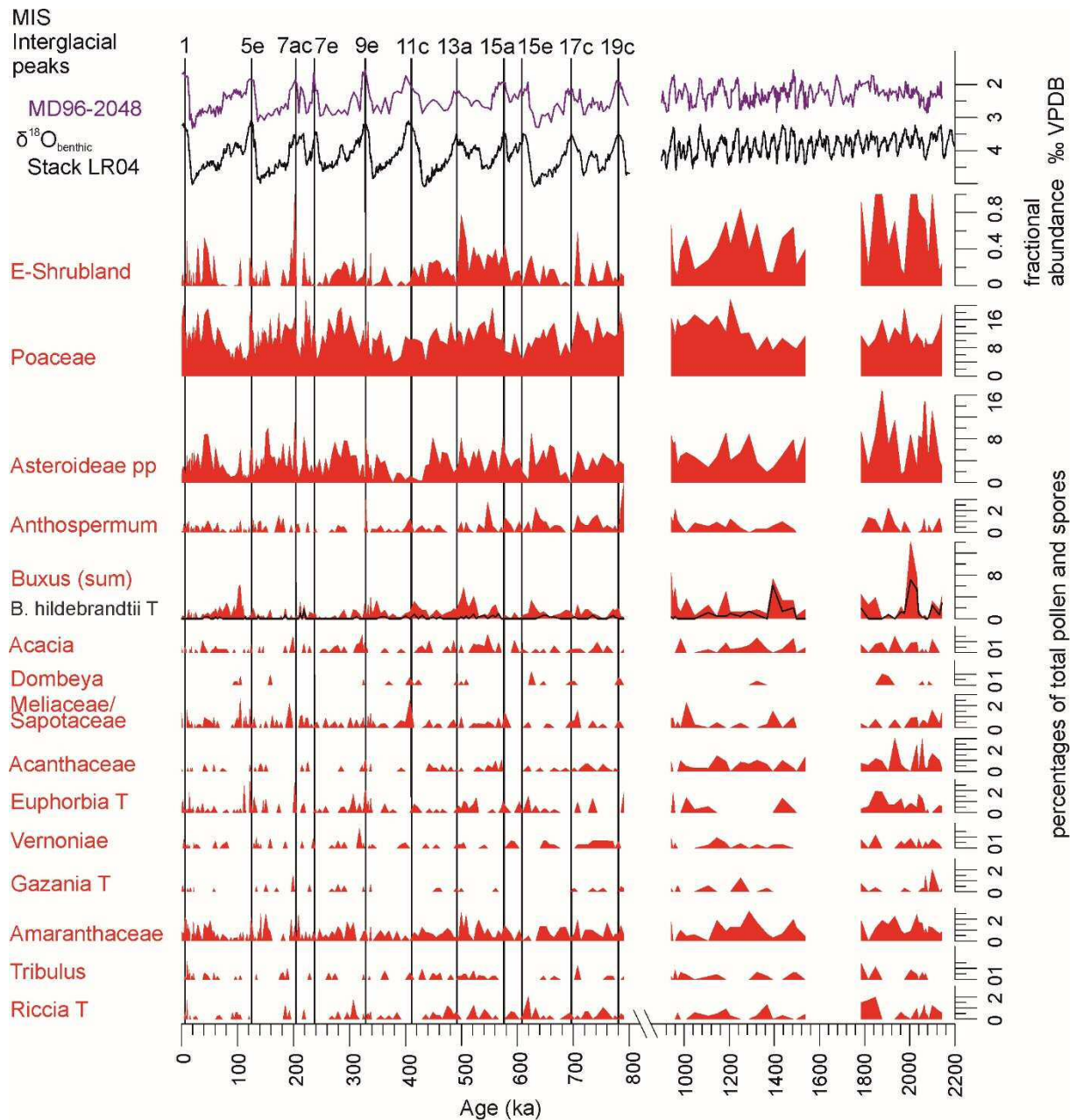
Supplementary Figures 1-4



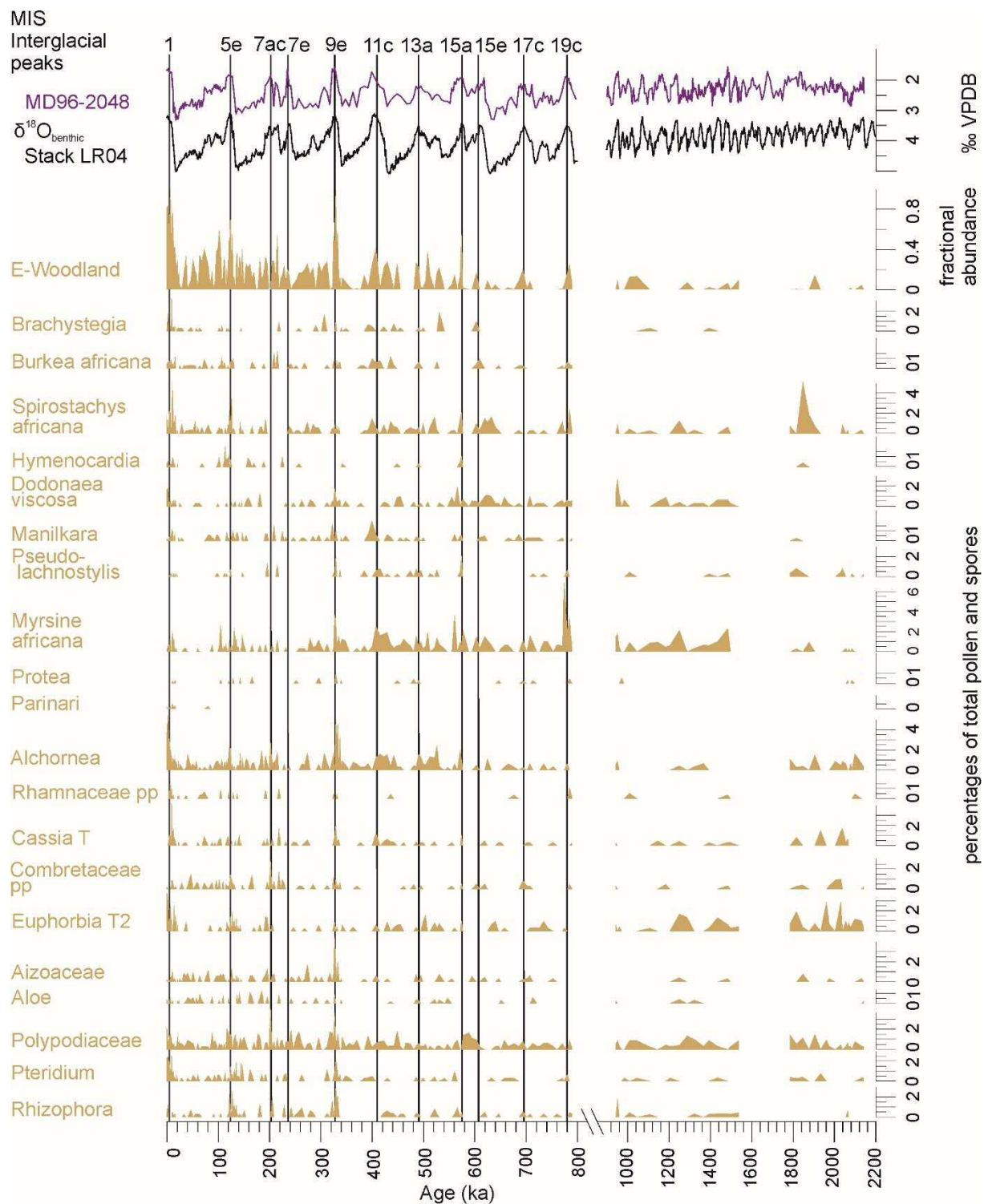
Supplementary Figure 1. Endmember assemblage scores and selected pollen taxa for E-Heathland (filled curves) against age in ka. On top Terminations and even-numbered marine isotope stages (MIS) of the Brunhes Chron are indicated. Stable oxygen isotopes of benthic foraminifers of Core MD96-2048 (violet line) and of global stack LR04 (black line, [Lisiecki & Raymo 2005](#)).



Supplementary Figure 2. Endmember assemblage scores and selected pollen taxa for E-Mountain-Forest (filled curves) against age in ka. On top Terminations and even-numbered marine isotope stages (MIS) of the Brunhes Chron are indicated. Stable oxygen isotopes of benthic foraminifera of Core MD96-2048 (violet line) and of global stack LR04 (black line, [Lisiecki & Raymo 2005](#)).



Supplementary Figure 3. Endmember assemblage scores and selected pollen taxa for E-Shrubland (filled curves) against age in ka. On top Terminations and even-numbered marine isotope stages (MIS) of the Brunhes Chron are indicated. Stable oxygen isotopes of benthic foraminifers of Core MD96-2048 (violet line) and of global stack LR04 (black line, [Lisiecki & Raymo 2005](#)).



1
2 Supplementary Figure 4. Endmember assemblage scores and selected pollen taxa for E-Woodland (filled curves) against age
3 in ka. On top Terminations and even-numbered marine isotope stages (MIS) of the Brunhes Chron are indicated. Stable
4 oxygen isotopes of benthic foraminifers of Core MD96-2048 (violet line) and of global stack LR04 (black line, [Lisiecki &](#)
5 [Raymo 2005](#)).