1 Effects of atmospheric CO_2 variability of the past 800 ka on the 2 biomes of Southeast Africa

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8 Abstract

- 9 Very little is known about the impact of atmospheric carbon dioxide pressure (pCO₂) on the shaping
- 10 of biomes. The development of *p*CO₂ throughout the Brunhes Chron may be considered a natural
- 11 experiment to elucidate relationships between vegetation and *p*CO₂. While the glacial periods show
- 12 low to very low values (~220 to ~190 ppmv, respectively), the pCO₂ levels of the interglacial periods
- 13 vary from intermediate to relatively high (~250 to more than 270, respectively). To study the
- 14 influence of *p*CO₂ on the Pleistocene development of SE African vegetation, we used the pollen
- 15 record of a marine core (MD96-2048) retrieved from Maputo Bay south of the Limpopo River mouth
- 16 in combination with stable isotopes and geochemical proxies. Applying endmember analysis, four
- 17 pollen assemblages could be distinguished representing different biomes: heathland, mountain
- 18 forest, shrubland and woodland. We find that the vegetation of the Limpopo River catchment and
- 19 the coastal region of southern Mozambique is not only influenced by hydroclimate but also by
- 20 temperature and atmospheric pCO_2 . Our results suggest that the extension of mountain forest
- 21 occurred during those parts of the glacials when pCO_2 and temperatures were moderate and that
- only during the colder periods when atmospheric *p*CO₂ was low (less than 220 ppmv) open
- 23 ericaceous vegetation including C4 sedges extended. The main development of woodlands in the
- area took place after the Mid-Brunhes Event (~430 ka) when interglacial *p*CO₂ levels regularly rose
- 25 over 270 ppmv.

26 Keywords

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

28 Short summary

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

32 Highlight

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

1 Introduction

- 2 Understanding the role of atmospheric carbon dioxide pressure (pCO₂) is paramount for the
- 3 interpretation of the of the paleo-vegetation record. The effects of low pCO_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 CO₂ 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. These
- 9 studies [opt cit.], however, mostly cover the last glacial-interglacial transition and do not examine
- 10 periods with intermediate pCO_2 such as during the Early Glacial (MIS 5a-d) or interglacials prior to
- 11 430 thousand years ago (430 ka). Comparing the vegetation record of subsequent climate cycles
- 12 showing different CO_2 levels might help to better understand the effects of pCO_2 on the vegetation.
- 13 During the Brunhes Chron (past 780 ka) the length of the glacial cycles became much longer lasting
- 14 roughly 100 ka due to a strong non-linear response of the ice sheets to solar forcing [Mudelsee &
- 15 <u>Stattegger 1997</u>]. Model experiments of <u>Ganopolski & Calov [2011]</u> indicate that low atmospheric
- 16 CO₂ concentrations are a prerequisite for the long duration of the glacial cycles of the past 800 ka.
- 17 Then, roughly mid-way through the Brunhes Chron, the amplitude of the climate cycles shifted with a
- 18 change in the maximum CO₂ concentration during interglacials.
- 19 This so-called Mid-Brunhes Event (MBE) [Jansen et al. 1986] also called Mid-Brunhes Transition -
- 20 occurred about 430 ka ago and marks the transition between interglacials characterized by rather
- low atmospheric CO₂ around 240 ppm (parts of Marine Isotope Stages (MIS) 19, 17, 15, 13) to
- interglacials in which CO₂ levels reached 270 ppmv or more (parts of MIS 11, 9, 7, 5, 1) [Lüthi et al.
- 23 2008, Bereiter et al. 2015]. The climate transition of the MBE has been extensively studied using
- 24 Earth System Models of Intermediate Complexity. Yin & Berger [2010] stress the importance of
- 25 forcing by austral summer insolation and Yin & Berger [2012] argue that the model vegetation (tree-
- 26 fraction) was forced by precession through precipitation at low latitudes. Both papers show the
- 27 necessity to include the change in atmospheric CO_2 in the explanation of the MBE [Yin & Berger,
- 28 <u>2010, 2012</u>]. <u>Yin [2013]</u>, however, concludes that it is not necessary to invoke a sudden event around
- 29 430 ka to explain the increased interglacial CO₂; the differences between interglacials before and
- 30 after the MBE can be explained by individual responses in Southern Ocean ventilation and deep-sea
- 31 temperature to various combinations of the astronomical parameters. On the other hand, statistical
- 32 analysis suggests a dominant role of the carbon cycle, which changed over the MBE [Barth et al.
- 33 <u>2018</u>]. <u>Paillard [2017]</u> developed a conceptual model of orbital forcing of the carbon cycle in which
- 34 sea-level fluctuations and the effects on carbon burial are decisive during shifts in the climate
- 35 system. Further modelling by <u>Bouttes et al. [2018]</u> showed qualitative agreement with the paleodata
- 36 of pre- and post-MBE interglacials but largely underestimated the amplitude of the changes.
- 37 Moreover, the simulated vegetation seems to counteract the effects of the oceanic response
- 38 [Bouttes et al. 2018]. Thus the vegetation, in particular at low latitudes, may play a crucial but poorly
- 39 understood role in the climate system.

- 1 Comparing records of pre- and post-MBE interglacials could offer insight in the interglacial climate at
- 2 different levels of CO₂ [Foley et al. 1994, Swan et al. 2010]. We define interglacials after PAGES
- 3 [2016] listing MIS 19c, 17c, 15a, 15e, 13a as pre-MBE and MIS 11c, 9e, 7e, 7a-c, 5e, 1 as post-MBE.
- 4 Currently, only a handful of vegetation records covering the entire Brunhes Chron have sufficient
- 5 temporal resolution to enable comparisons between interglacials before and after the Mid-Brunhes
- 6 transition. These records are from the eastern Mediterranean, the Colombian Andes [PAGES 2016],



Figure 1. Upper panel: map of southern Africa with the main phytochoria after <u>White (1983)</u>. 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.

1 West and East Africa [Dupont et al. 1989, Miller & Goslin 2014, Castañeda et al. 2016, Johnson et al.

- 2 <u>2016</u>, Ivory et al. 2018, Owen et al. 2018]. The Andean pollen record is strongly influenced by the
- 3 immigration of oak from North America during MIS 12 [Torres et al. 2013]. For the eastern
- 4 Mediterranean a decline in plant diversity is observed at Tenaghi Phillipon (Greece) where the
- 5 modern Mediterranean oak forests gradual emerged in the interglacials after MIS 16 but before the
- 6 MBE [Tzedakis et al. 2006, 2009]. The West African record of Lake Bosumtwi in Ghana allows
- 7 identification of six forest assemblages since 540 ka related to the interglacials of MIS 13, 11, 9, 7, 5e,
- 8 and 1. The forests assemblage of MIS 13, however, does not show a strong contrast with those of the
- 9 interglacials after the MBE [Miller & Goslin 2014]. The marine pollen record of ODP Site 658 off Cape
- 10 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
- 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
- 14 Chinese loess sections indicate interglacial-glacial variability in the C3-C4 proportions of the
- 15 vegetation [Lyu et al. 2018, Sun et al. 2019]. However, the latter records do not show a prominent
- 16 vegetation shift over the MBE.
- 17 For East Africa two terrestrial records and a marine one are available. From Lake Malawi, Johnson et
- 18 <u>al. [2016]</u> infer wetter conditions and increased woodland vegetation between 800 and 400 ka based
- 19 on the stable carbon isotopic composition of plant wax shifting from less to more strongly depleted
- values. Also from Lake Malawi, <u>Ivory et al. [2018]</u> published a pollen record of the past 600 ka
- 21 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
- 25 *Podocarpus* decreased over the MBE, while open grassy vegetation and salinity of the lake increased
- 26 [Owen et al. 2018]. Neither the Lake Malawi nor the Lake Magadi records show dominant
- 27 interglacial-glacial variability.
- 28 The marine record retrieved south of the Limpopo River mouth (Core MD96-2048) allows inferences
- 29 about vegetation and climate in the catchment area of the Limpopo River draining large areas of
- 30 South Africa, Botswana, Zimbabwe and Mozambique. Based on sediment chemistry, <u>Caley et al.</u>
- 31 [2018] reported the effects of increased summer insolation in increased fluvial discharge and
- 32 variability associated with eccentricity, which modulates precession amplitudes. Superimposed on
- 33 the orbital-scale precipitation variability, a long-term trend from 1000 to 600 ka towards increased
- 34 aridity in southeastern Africa was found <u>[Caley et al. 2018]</u>. The plant leaf wax carbon isotopic
- 35 (hereafter $\delta^{13}C_{wax}$) record of the same core was originally interpreted as reflecting a trend toward 36 increasingly drier glacials and wetter interglacials over the past 800 ka [Castañeda et al. 2016].
- Additionally, the average 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
- 39 during the post-MBE interglacials [Castañeda et al. 2016]. Thus, a pollen record of MD96-2048 has
- 40 the potential to register the changes in interglacial vegetation cover over the MBE. We might expect
- 41 a change of Southern Hemisphere vegetation being less ambiguous than the changes found on the
- 42 Northern Hemisphere (see above), because modelling indicates that the effects of the MBE were
- 43 more pronounced on the Southern Hemisphere [Yin & Berger 2010]. Until now, the palynology of
- only the last 350 ka has been published [Dupont et al. 2011] and, therefore, here we extend the
- 45 pollen record of MD96-2048 to cover the past 800 ka in sufficient resolution. As described below, our
- 46 new palynology results have led to the re-interpretation of the MD96-2048 $\delta^{13}C_{wax}$ record [Castañeda
- 47 <u>et al. 2016]</u>.

1 Previous work on Core MD96-2048

- 2 The sediments of MD96-2048 were retrieved in the middle of the Maputo Bight (Figure 1) from the
- 3 southern Limpopo cone forming a depot center that has been build up at least since the Late
- 4 Miocene [Martin 1981]. The site collects terrestrial material including pollen and spores mostly from
- 5 the rivers that discharge into the Maputo Bight of which the Limpopo River is the biggest draining
- 6 large areas of northern South Africa and southern Mozambique. Apart from the offshore winds
- 7 descending from the interior plateau, so-called Bergwinds, the predominant wind direction is
- 8 landward [Tyson & Preston-Whyte 2000] and aeolian input of terrestrial material is probably minor.
- 9 Thus, pollen source areas would cover the region north of the Maputo Bight in southern
- 10 Mozambique and the region west of Maputo of the Lebombo hills and the Drakensberg Escarpment
- 11 [Dupont et al. 2011].
- 12 A wide variety of measurements have been performed on MD96-2048 sediments. <u>Caley et al. [2011,</u>
- 13 <u>2018</u>] 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]
- 15 for the past 2200 ka. Trace element (Mg/Ca ratios) of the planktic foraminifer *Globigernoides ruber*
- 16 *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
- 18 performed over the total core length, of which the iron-calcium ratios, ln(Fe/Ca), were used to
- 19 estimate fluvial terrestrial input variability [Caley et al., 2018]. At millennial resolution, higher plant
- 20 leaf wax (*n*-alkane) concentrations and ratios and compound specific stable carbon isotopes ($\delta^{13}C_{wax}$)
- 21 provided a record of vegetation changes in terms of open versus closed canopy and C4 versus C3
- 22 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(Fe/Ca), was used to reconstruct rainfall and Limpopo River runoff during the past 2.0 Ma.
- 25 Present-day climate and vegetation
- 26 Modern climate is seasonal with the rainy season in summer (November to March). Yearly
- 27 precipitation ranges from 600 mm in the lowlands to 1400 mm in the mountains, whereby rains are
- 28 more frequent along the coast under the influence of SSTs [Jury et al. 1993, Reason & Mulenga
- 29 <u>1999</u>]. Annual average temperatures range from 24 to 16°C but in the highlands clear winter nights
- 30 may be frosty.
- 31 The modern vegetation of this area belongs to the forest, Highveld grassland, and savannah biomes
- 32 and also includes azonal vegetation (Figure 1) [Dupont et al. 2011 and references therein]. The
- 33 natural potential vegetation of the coastal belt is forest, although at present it is almost gone; north
- 34 of the Limpopo River mouth rain forests belong to the Inhambane phytogeographical mosaic and
- 35 south of the Limpopo River the forest belongs to the Tongaland-Pondoland regional mosaic [White
- 36 <u>1983</u>]. The vegetation of the northern part of the Tongaland-Pondoland region is the Northern
- 37 Coastal Forest [Mucina & Rutherford 2006]. Semi-deciduous forest is found in the Lebombo hills
- 38 [Kersberg 1996]. Afromontane forest and Highveld grasslands grow along the escarpment and on the
- 39 mountains. The savannahs of the Zambezian phytogeographical region including e.g. the miombo dry
- 40 forest occur further inland [White 1983]. Azonal vegetation consists of freshwater swamps, alluvial,
- 41 and seashore vegetation and mangroves [Mucina & Rutherford 2006].

42 Material and Methods

- 43 Pollen analysis of the 37.59 m long core MD96-2048 (26°10'S 34°01'E, 660m water depth) was
- 44 extended with 65 samples down core to 12 m (790 ka). Average sampling distance for the Brunhes
- 45 part was 7 cm reaching an average temporal resolution of 4 ka according to the age model based on

- 1 the stable oxygen isotope stratigraphy of benthic foraminifers [Caley et al. 2011, 2018]. Two older
- 2 windows have been sampled; 20 samples between 15 and 26 m (943-1537 ka) and 19 samples
- 3 between 30 and 36 m (1785-2143 ka) were taken with an average resolution of 31 and 20 ka,
- 4 respectively.
- 5 Pollen preparation has been described in [Dupont et al. 2011]. In summary, samples were decalcified
- 6 with HCl (~10%), treated with HF (~40%) for two days, ultrasonically sieved over an 8-μm screen and,
- 7 if necessary, decanted. The samples were spiked with two Lycopodium spore tablets (either of batch
- 8 #938934 or batch #177745). Residues were mounted in glycerol and pollen and spores examined at
- 9 400x or 1000x magnification. Percentages are expressed based on the total of pollen and spores
- 10 ranging from over 400 to 60 only in six samples this sum amounts to less than 100. Confidence
- 11 intervals (95%) were calculated after Maher [1972, 1981]. Pollen have been identified using the
- 12 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: elmental Fe/Ca ratios [Caley et al. 2018]; less negative values indicate relatively wetter conditions, $\delta^{13}C_{wax}$ of the *n*-alkane C_{31} [Castañeda et al. 2016, Caley et al. 2018]; less negative values of around -24‰ indicae 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. <u>Bonnefille</u>
 & Riollet 1980, Scott <u>1982</u>, Köhler & Brückner <u>1982</u>, <u>1989</u>, Schüler & Hemp <u>2016</u>].
- 15 We assigned pollen taxa to groups such as riparian, woodland, forest, etc. (Supplementary Table 1)
- using information given by <u>Scott [1982]</u>, White [1983], Beentje [1994], Kersberg [1996], Coates-
- 17 Palgrave [2002], Vincens et al. [2007]. Additionally, we carried out a multivariate analysis in the form
- 18 of an endmember model unmixing procedure [Weltje, 1997], the statistics of which are specifically
- 19 designed for the treatment of percentage data. We regard the pollen percentages as a series of
- 20 pollen assemblage mixtures, whereby each modelled endmember may be interpreted as the

- 1 representation of one or more biomes. This linear mixing model can be compared to a ternary
- 2 diagram but allowing for more than three axes. We use a version of the unmixer algorithm
- 3 programmed in MATLAB by Dave Heslop in 2008. Taxa occurring in 6 or more samples (listed in
- 4 Supplementary Table 2) were used in the endmember modelling (148 of 231 taxa in 220 samples).
- 5 We selected a model with four components explaining more than 95% of the variance (r² =0.953).
- 6 Iteration was stopped at 1000x resulting in a convexity at termination of -1.6881. Significance level at
- 7 99% for taxa to score on the assemblages was 0.018.
- 8 To study the correlations between different parameters, we used a linear regression model (least
- 9 square regression) on linearly interpolated values (5 ka steps) from 0 to 790 ka. Correlation
- 10 coefficients are given in Table 1. For interpolation and testing the correlation, we used the package
- 11 PAST [Hammer et al. 2001].

12 Result and Discussion

13 Terrestrial input and provenance of the C4 plant wax

14 Pollen percentages of Cyperaceae (sedges) and Poaceae (grasses) are plotted in Figure 2 together

- 15 with the $\delta^{13}C_{wax}$ of the C₃₁ *n*-alkane and XRF-scanning data, ln(Fe/Ca), the natural logarithm of
- 16 elemental ratios of iron over calcium. Comparing the records of Cyperaceae and $\delta^{13}C_{wax}$ reveals that
- 17 high relative amounts of C4 plant material co-varied with increased representation of sedges. They
- also co-varied with higher terrestrial input indicated by In(Fe/Ca), and increased precipitation as
- 19 suggested by deuterium of the C₃₁*n*-alkane [Caley et al., 2018]. We substantiated the correlations for
- 20 the Brunhes Chron between pollen percentages, leaf waxes and elemental ratios in Table 1. Leaf wax
- 21 data are after <u>Castañeda et al. [2016]</u> including Average Chain Length (ACL) of the C₂₇ C₃₃*n*-alkanes,
- 22 the ratio of $C_{31}/(C_{31}+C_{29})$ and $\delta^{13}C_{wax}$. XRF ln(Fe/Ca) ratios are from <u>Caley et al. [2018]</u>. Significant
- 23 correlation is found between the leaf wax parameters and Cyperaceae data but not between $\delta^{13}C_{wax}$
- 24 (indicative of C4 inputs) and Poaceae pollen percentages although a correlation exists between
- 25 Cyperaceae and Poaceae percentages. While the sedge pollen percentages fluctuate between 10 and
- 26 50% (mostly > 20%), the percentages of grass pollen are always lower than 20%. Such low grass
- 27 pollen values have not been found adjacent C4 grass dominated biomes (mainly savannahs) on the
- 28 western side of the continent [Dupont 2011]. It is, therefore, likely that in sediments of MD96-2048
- 29 the C4 component of the plant wax originated from C4 sedges rather than from C4 grasses.
- 30 South Africa has 68 species of Cyperaceae (sedges) of which 28 use the C4 pathway (among the 10
- 31 *Cyperus* species 8 are C4) predominantly growing in the northern part of the country [Stock et al.
- 32 <u>2004</u>]. They are an important constituent of tropical swamps and riversides [Chapman et al. 2001].

Table 1. Correlation coeffients 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 $C_{31}/(C_{31} + C_{29})$, and stable carbon isotope composition of the $C_{31}n$ -alkane ($\delta^{13}C_{wax}$) after Castañeda et al. [2016]. Cyperaceae and Poaceae pollen percentages (of total pollen and spores) after Dupont et al. [2011] and this study. In(Fe/Ca) data after Caley et al. [2018].

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

- 1 An inventory of six modern wetlands between 500 and 1900m in KwaZulu Natal shows that C4
- 2 grasses dominate the dry surroundings of the wetlands at all altitudes [Kotze & O'Connor 2000]. In
- 3 the wet parts of the wetlands, however, C4 sedges may make up to 60% of the vegetation cover at
- 4 550 m. At higher altitudes the coverage of C4 sedges declines [Kotze & O'Connor 2000].
- 5 Cyperaceae pollen concentration (Figure 3) and percentages correlate with ln(Fe/Ca) and with
- $\delta^{13}C_{wax}$ (Table 1, Figure 2). The ratios of terrestrial iron over marine calcium can be interpreted as a
- 7 measure for terrestrial input, which in this part of the ocean is mainly fluvial. Correlation between
- 8 increased fluvial discharge and increased C4 vegetation as well as increased Cyperaceae pollen has
- 9 been reported from sediments off the Zambezi [Schefuß et al. 2011, Dupont & Kuhlmann 2017].
- 10 Moreover, a fingerprint of C4 sedges was found in Lake Tanganyika [Ivory & Russel 2016]. As a
- 11 consequence, material (leaf waxes and pollen) from the riverine vegetation is probably better
- 12 represented than that from dry and upland vegetation. These results corroborate the
- 13 reinterpretation of the $\delta^{13}C_{wax}$ record, in which the increased representation of C4 plants (*n*-alkanes
- 14 enriched in ¹³C) 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 <u>Castañeda et al. [2016]</u> had interpreted increased C4 inputs as reflecting
- 10 <u>et al., 2010</u>. Previously <u>castaneda et al. [2010]</u> nau interpreted increased C4 inputs as reflecting
- 17 increased aridity.
- 18 Relatively low values of Cyperaceae pollen and Fe/Ca ratios are found for most interglacials of the
- 19 Brunhes Chron (Figures 2 and 3), which could be interpreted as an effect of sea-level high-stands.
- 20 However, <u>Caley et al. [2018]</u> demonstrated that the fluvial discharge is not related to sea-level
- 21 changes. From the bathymetry of Maputo Bay, strong influence of sea-level is also not expected
- 22 because the shelf is not broad and the locality of Core MD96-2048 is relatively remote on the
- 23 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
- 25 has not changed direction during glacial times. Thus, fluvial discharge was probably low during
- 26 interglacials (among other periods), which might be the combined result of more evapotranspiration
- 27 and less precipitation. Despite drier conditions, the representation of woodland and dry forest is
- relatively high during the interglacial periods (Figure 3, see also next section).
- 29 Endmembers representing vegetation on land
- 30 Palynological results have been published for the past 350 ka [Dupont et al. 2011] providing a
- 31 detailed vegetation record for the past three climate cycles. Pollen and spore assemblages could be
- 32 characterized initially by three endmembers via endmember modelling (EM1, EM2, EM3). The
- 33 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
- 35 percentages of Cyperaceae (sedges), Ericaceae (heather) and other plants of open vegetation and
- 36 abundant during full glacial stages. EM3 constituted of pollen from woodland, forest, and coastal
- 37 vegetation and was interpreted to represent a mix of several vegetation complexes.

- 1 We repeated the endmember modelling for the extended record covering the entire Brunhes Chron
- 2 and the two early Pleistocene windows. The analysis of the extended dataset gave compatible results
- 3 with the previous analysis (Dupont et al. 2011). The main difference is that the longer sequence
- 4 allowed to distinguish two assemblages of interglacial vegetation. In terms of analysis, the
- 5 cumulative increase of explanatory power lessened after four (instead of three) endmembers and a
- 6 model with four endmembers was chosen. We used the scores of the different pollen taxa on the
- 7 endmember assemblages for our interpretation of the endmembers (list of taxa and scores in
- 8 Supplementary Tables 1 and 2). This interpretation is summarized in Table 2. To distinguish between
- 9 the previous and current analysis (which show strong similarities), we have given new names to the
- 10 endmember assemblages reflecting our interpretation: E-heathland, E-Mountain-Forest, E-
- 11 Shrubland, E-Woodland. A selection of pollen percentage curves are plotted together with each
- 12 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]; $\delta^{18}O_{benthic}$ of Core MD96-2048 [Caley et al. 2018]; Interglacial peaks after PAGES [2016]. VPDB: Vienna Pee Dee Belemnite.

- 13 E-Heathland. Of the four endmember assemblages (Figure 3), one endmember had a counterpart in
- 14 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
- 16 'E-Heathland', which is dominated by Cyperaceae (sedges) pollen percentages followed by Ericaceae

- 1 (heather) pollen and hornwort (Anthocerotaceae) spores (Table 2). Also *Lycopodium* (clubmoss)
- 2 spore, Restionaceae and Stoebe-type pollen percentages score highest on this endmember. The E-
- 3 Heathland assemblage represents a Fynbos-like open vegetation growing during full glacials. Other
- 4 pollen records from SE Africa also indicate an open ericaceous vegetation with sedges and
- 5 Restionaceae during glacial times [Scott 1999, Dupont & Kuhlmann 2017]. The record of MD96-2048
- 6 testifies that this type of open glacial vegetation regularly occurred since at least two million years.

7 **E-Mountain-Forest.** Like the endmember EM1 [Dupont et al. 2011] of the previous analysis, one

- 8 endmember is dominated by *Podocarpus* (yellow wood) pollen percentages (Table 2). The
- 9 assemblage is enriched by pollen of *Celtis* (hackberries) and *Olea* (olive trees) accompanied by
- 10 undifferentiated fern spores. The interpretation as an assemblage representing mountain forest is
- 11 rather straightforward and we name the assemblage 'E-Mountain-Forest'. The fractional abundance
- 12 of the E-Mountain-Forest is also high in glacials of the Brunhes Chron but not during the extreme
- 13 glacial stages, when temperatures and pCO_2 are particularly low (Figure 3). It is low in the early -
- 14 Pleistocene parts of the record.
- 15 **E-Shrubland.** 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
- 17 [Dupont et al. 2011]. One endmember groups together 44 pollen taxa, mostly from coastal and dune
- 18 vegetation, which we name 'E-Shrubland'. It includes pollen of Asteraceae and Poaceae (grasses).
- 19 The latter are not very specific as grass pollen values score almost as high on other endmember
- 20 assemblages (E-Heathland and E-Woodland). Several taxa scoring on this endmember are known
- 21 from coastal or halophytic settings such as Gazania-type, Amaranthaceae, Tribulus, Acanthaceae and
- 22 Euphorbia-type. Arboreal taxa in this assemblage are Dombeya, Acacia, Meliaceae/Sapotaceae (Table
- 23 2). The most typical taxa are the *Buxus* species. We distinguished three types of *Buxus* pollen: *B*.
- 24 macowani type, B. hildebrandtii type and B. cf. madagascarica [Köhler & Brückner 1982, 1989]. B.
- 25 madagascarica 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
- 27 nowadays is found in Somalia and Ethiopia and *B. macowani* is native in South Africa. The record of
- 28 M96-2048 indicates that these *Buxus* species were more common in the early Pleistocene than
- 29 during the Brunhes Chron (Figure 3).

Table 2: Interpretation of the enamembers				
Endmember	Main pollen taxa			
E-Heathland	Podocarpus, Celtis, Olea			
E-Mountain-Forest	Cyperaceae, Ericaceae, Phaeoceros, Restionaceae, Stoebe type, Anthoceros,			
	Typha Lycopodium, Restionaceae			
E-Shrubland	Poaceae, Asteroideae, Buxus, Amaranthaceae, Euphorbia, Meliaceae-			
	Sapotaceae, Acacia, Riccia type, Tribulus, Acanthaceae pp, Asteraceae			
	Vernoniae, Hypoestes-Dicliptera type, Gazania type, Dombeya			
E-Woodland	Alchornea, Spirostachys africana, Pteridium type, Polypodiaceae, Myrsine			
	africana, Cassia type, Rhizophoraceae, Aizoaceae, Combretaceae pp, Manilkara,			
	Burkea africana, Brachystegia, Dodonaea viscosa, Pseudolachnostylis,			
	Hymenocardia, Aloe, Rhamnaceae pp, Protea, Parinari			

Table 2. Interpretation of the endmembers

- 31 **E-Woodland.** The last endmember, which we name 'E-Woodland', groups together 39 pollen taxa
- 32 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
- 34 are woodland trees. *Protea* (sugarbush) and *Myrsine africana* (Cape myrtle) grow more upland and
- 35 *Alchornea* is a pioneer forest tree often growing along rivers. Others include wide-range woodland
- 36 taxa such as Combretaceae species. The occurrence of pollen of *Brachystegia* (miombo tree), *Burkea*
- 37 *africana, Spirostachys africana* and *Hymenocardia* in this assemblage is indicative of Miombo dry

- 1 forest and woodland. The assemblage additionally includes Rhizophoraceae pollen from the coastal
- 2 mangrove forest (Table 2). The fractional abundance of the E-Woodland assemblage is low during the
- 3 early Pleistocene, increased during the interglacials prior to the MBE and had maximum values
- 4 during Interglacials 9e, 5e, and 1 (Figures 3, 4). These interglacials also exhibited maximum
- 5 percentages of arboreal pollen excluding *Podocarpus*.
- 6 In summary, the endmember analysis indicates a very stable open ericaceous vegetation with
- 7 partially wet elements such as sedges and Restionaceae characterizing the landscape of full glacials
- 8 (when global temperatures and *p*CO₂ were lowest). During the less extreme parts of the glacials,
- 9 mountain *Podocarpus* forest was extensive as in most mountains of Africa [Dupont 2011, Ivory et al.
- 10 <u>2018</u>]. On the other hand, interglacials were characterized by coastal shrubs. In the course of the
- 11 Brunhes, the woody component, which was relatively weak before the MBE, became more and more
- 12 important reflecting the same long-term trend found in the leaf wax records [Castañeda et al. 2016].
- 13 It is likely that the Miombo dry forest and woodland migrated into the region in the successive
- 14 interglacials of the Brunhes Chron. Particularly during Interglacials 9e and 1 the area might have been
- 15 more forested than during the older interglacials of the Brunhes Chron.

16 Long-term trends in vegetation and climate of East Africa

- 17 The region of the Limpopo River becoming more and more wooded in the course of successive
- 18 interglacials [Castañeda et al. 2016] somewhat paralleled the conditions around Lake Malawi
- 19 [Johnson et al. 2016]. However, around Lake Malawi, forested phases of either mountain forest,
- 20 seasonal forest, or Miombo woodland alternating with savannahs occurred during both glacial and
- 21 interglacial stages [Ivory et al. 2018]. Also in contrast to the Lake Malawi record, the MD96-2048
- 22 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
- 24 southern Mozambique.
- 25 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-
- 28 Brunhes transition [Owen et al. 2018]. Antiphase behavior of SE African climate with that of West
- and East Africa emphases the importance of the average position of the tropical rainbelt shifting
- 30 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
- 32 over the entire Brunhes Chron.
- 33 The Lake Malawi pollen record as well as that of the equatorial Lake Magadi in Kenya [Owen et al.
- 34 <u>2018</u>] 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
- 36 Southern Hemisphere north of ~15°S the hydrological regime had more effect on the vegetation than
- 37 changes in temperature, while further south the impact of glacial-interglacial variability on the
- 38 vegetation increased.

39 Effects of atmospheric *p*CO₂

- 40 While the hydroclimate of the region shows precession variability [Caley et al. 2018], the vegetation
- 41 shows a glacial-interglacial rhythm (Supplementary Information) indicating that besides hydrology,
- 42 temperature and/or atmospheric CO₂ levels were important drivers of the vegetation development.
- 43 Combining the results of the pollen assemblages with stable carbon isotopes and elemental
- 44 information indicates that during interglacials the region of SE Africa (northern South Africa,

- 1 Zimbabwe, southern Mozambique) was less humid. This is in accordance with other paleoclimate
- 2 estimates for the region [see reviews by Simon et al. 2015, Singarayer & Burrough 2015].
- 3 The interglacial woodlands (represented by E-Woodland, Figure 4) would probably have grown under
- 4 warmer and drier conditions than the glacial mountain forest (represented by E-Mountain-Forest).
- 5 The increase in maximum pCO_2 levels during the post-MBE interglacials might have favored tree
- 6 growth as higher pCO_2 levels would have allowed decreased stomatal conductivity and thus relieved
- 7 drought stress [Jolly & Haxeltine 1997]. Woodlands would have expanded at the cost of mountain
- 8 forest during 11c, 9e, 5e and 1, and to a lesser extend during 7e and 7c, when temperatures and
- 9 pCO_2 were high (Figure 4). It might be only after interglacial pCO_2 levels rose over ~270 ppmv that
- 10 Miombo woodland could fully establish in the area during the warm and relatively dry post-MBE
- 11 interglacials.
- 12 The glacial stages showed the expansion of either mountain forest or heathland. The record indicates
- 13 extension of mountain forests in SE Africa during those parts of the glacial stages with low
- 14 temperatures and atmospheric *p*CO₂ exceeding ~220 ppmv (Figure 5). If low temperatures were the
- 15 only driver of the extension of mountain forests, further spread into the lowlands during the coldest
- 16 glacial phases should be expected. Instead, when pCO_2 dropped below ~220 ppmv during those
- 17 colder glacial periods, mountain forest declined, in particular during MIS 18, 16, 14, 8, 6, and 2. A



Figure 4: Comparing pollen assembages E-Mountain-Forest, E-Woodland and E-Shrubland with atmospheric CO₂ [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]. CO₂-levels of 220 and 270 ppmv are indicated with green-red shading. Grey shading highlight periods with maximum atmospheric CO₂ and maximum values of the sum of E-Woodland and E-Mountain-Forest. VPDB: Vienna Pee Dee Belemnite.

- 18 picture emerges of cool glacial stages in SE Africa in which tree cover broke down when atmospheric
- 19 *p*CO₂ became too low. Additionally, mountain forests were important during the Interglacials 19c,
- 20 17c, 15e, 15a, 13a, and 7e, in which *p*CO₂ and Antarctic temperatures were subdued.

- 1 With an inverse modelling technique, <u>Wu et al. [2007]</u> estimated the climate inputs for the
- 2 vegetation model BIOME4 using as information the biome scores of pollen records from equatorial
- 3 East African Mountains. <u>Wu et al.</u> found that lowering of the tree line under glacial conditions (1-3°C
- 4 lower temperatures, less precipitation, 200 ppmv *p*CO₂) depended hardly on temperature but
- 5 primarily on increased aridity and somewhat on lower pCO_2 , whereby lower pCO_2 amplified the
- 6 effects of water limitation. However, <u>Izumi & Lézine [2016]</u> found contrasting results using pollen
- 7 records of mountain sites on both sides of the Congo basin. At any rate, the lack of trees in the
- 8 Southeast African Mountains during glacial extremes is unlikely the result of drought, because our
- 9 record indicates that climate conditions in SE Africa were less dry during glacials than during
- 10 interglacials (the post-MBE interglacials in particular). Instead, C4 sedges being an important
- 11 constituent of the ericaceous fynbos-like vegetation increased during glacials when atmospheric
- 12 *p*CO₂ and temperatures were low (Figure 5). However, low temperatures are not particularly
- 13 favorable for C4 sedges as indicated by the altitudinal distribution of C4 sedges in modern wetlands
- 14 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 CO₂ concentrations
- 16 rather than of low temperatures.
- 17 Pollen records of ericaceous vegetation suggest an extensive open vegetation existing in the East
- 18 African Mountains [e.g. <u>Coetzee 1967, Bonnefille & Riollet 1988, Marchant et al. 1997, Debusk 1998,</u>
- 19 Bonnefille & Chalié 2000] and in SE Africa and Madagascar [e.g. Botha et al. 1992, Scott 1999, Gasse
- 20 and Van Campo 2001, Scott & Tackeray 1987] during the last glacial. In our study, ericaceous fynbos-
- 21 like vegetation (E-Heathland) was found for those parts of the glacials having lower (less than ~220
- ppmv) atmospheric *p*CO₂ (Figure 5). Exceptions were found for MIS 12 and 14 when the difference of
- pcO₂ with that of the preceding stage was small [Bereiter et al. 2015]. Dupont et al. [2011] argued
- 24 that increase of C4 vegetation as the result of low pCO_2 was unlikely because no extension of grasses
- 25 was recorded. However, this argument is flawed if sedges dominantly constituted the C4 vegetation
- 26 in the area. We also note that in many parts of South Africa, no substantial increase of C4 grasses
- 27 occurred but that many sites suggest an expansion of C3 grasses during the Last Glacial Maximum
- 28 [Scott 2002].
- 29 As climate was wetter during most of the glacials in this part of the world, the question arises about
- 30 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 (see also the correlation between SST and EM2 in <u>Dupont et al. 2011</u>). The correlation with
- 33 SST, however, is problematic. <u>Singarayer & Burrough [2015]</u> argued that the control of the Indian
- 34 Ocean SSTs on the precipitation of South Africa shifted from a positive correlation during the
- 35 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
- 37 causing a wetter region over the western Indian Ocean but also weaker easterly winds to transport
- 38 moisture inland. To question the link between SST and precipitation in SE Africa even further, <u>Caley</u>
- 39 <u>et al. [2018]</u> found that the precession signature in the river discharge proxy [ln(Fe/Ca), see also
- 40 Supplementary Information] was absent in the SST record from the same core. SE Africa would have
- 41 been more humid during glacials when the temperature difference between land and sea increased.

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



Figure 5: Comparing Cyperaceae pollen percentages and fractional abundances of the glacial pollen assembages E-Mountain-Forest and E-Heathland with atmospheric CO₂ [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, glacial marine isotope stages (MIS) and stable oxygen isotopes of benthic foraminifera ($\delta^{18}O_{benthic}$) of MD96-2048 [Caley et al. 2011]. CO₂-levels of 220 and 270 ppmv are indicated with blue-green-red shading. Grey shading highlight periods with minimum atmospheric CO₂, minimum values of E-Mountain-Forest and Cyperaceae pollen, and maximum values of E-Heathland. VPDB: Vienna Pee Dee Belemnite.

10 Conclusions

- 11 Palynology in combination with sediment chemistry and carbon isotope analysis of leaf waxes carried
- 12 out on the marine sediments of MD96-2048 retrieved from the Limpopo River cone in the Maputo
- 13 Bay (SE Africa) allowed a detailed reconstruction of the biome developments over the Brunhes Chron
- 14 and comparison with earlier Pleistocene vegetation of SE Africa.
- 15 Using endmember modelling, we could distinguish four pollen assemblages: E-Heathland, E-
- 16 Mountain-Forest, E-Shrubland, E-Woodland. The open sedge-rich and ericaceous vegetation

- 1 represented by E-Heathland ocurred during those parts of the glacials with lower temperatures and
- 2 atmospheric *p*CO₂. *Podocarpus*-rich mountain forest represented by E-Mountain-Forest extended
- 3 during the less extrem parts of the glacials. E-Shrubland represents a shrublike vegetation with
- 4 coastal elements and *Buxus* species and mainly occurred during the earlier Pleistocene (before 1 Ma).
- 5 E-Woodland represents interglacial woodlands, Miombo woodland in particular, becoming more and
- 6 more important in the succesive interglacial stages of the Brunhes Chron and dominated the post-
- 7 MBE interglacials.
- 8 Our results indicate the influence of atmospheric *p*CO₂ fluctuations on the shaping of the biomes in
- 9 SE Africa during the Brunhes Chron. We argue that (1) the precessional rhythms of river discharge
- 10 compared to the interglacial-glacial biome variability indicates that hydroclimate cannot be the only
- 11 driver of vegetation change. The other options of forcing mechanisms on interglacial-glacial time-
- 12 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
- 15 mainly derives from the sedges. (3) The expansion of C4 sedges during the colder periods of the
- 16 glacials is unlikely to result from lower temperatures. Thus, during the colder phases of the glacials,
- 17 low atmospheric pCO_2 might have favored the expansion of C4 sedges. (4) The confinement of
- mountain forest to the glacial periods with moderate temperatures and moderate pCO_2 , and the lack
- 19 of extension into the lowlands of mountain forest during the colder periods, suggests that low pCO_2
- became restrictive to the forest. Moutain forests could thrive during glacials as long as pCO_2 levels
- 21 exceeded ~220 ppmv. (5) Based on the elemental composition as a proxy for river discharge
- 22 [In(Fe/Ca)], we estimate the post-MBE interglacials as the drier intervals of the sequence.
- 23 Nevertheless woodland extended during those periods, which we attribute to increased
- temperatures and pCO_2 . Atmospheric pCO_2 levels over 250 ppmv might have been a prerequisite for
- 25 the establishment of the Miombo woodlands in SE Africa, which extended during the post MBE
- 26 interglacials.
- 27 The vegetation record of the Limpopo catchement area shows a greater impact of glacial-interglacial
- variability, mainly driven by CO₂ fuctuations, and less influence of hydroclimate compared to the
- 29 more equatorial records of Lake Malawi and Lake Magadi. The long-term trend of increased
- 30 woodiness in the course of the Brunhes Chron parralleled that of Lake Malawi but constrasted Lake
- 31 Magadi suggesting a long-term southward shift in the average position of the tropical rainbelt.

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- 36 application.

37 Data availability

- 38 Pollen counts are available at https://doi.pangaea.de/10.1594/PANGAEA.897922.
- 39 Previously published data can be retrieved at https://doi.pangaea.de/10.1594/PANGAEA.895364;
- 40 https://doi.pangaea.de/10.1594/PANGAEA.895361;
- 41 https://doi.pangaea.de/10.1594/PANGAEA.895362;
- 42 https://doi.pangaea.de/10.1594/PANGAEA.863919;
- 43 https://doi.pangaea.de/10.1594/PANGAEA.895357.

1 Author contributions

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

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1 Supplement

2 REDFIT frequency analysis

- 3 We conducted a frequency analysis on the data of the ln(Fe/Ca) ratios, the E-Heathland fractional
- 4 abundance scores, and the Cyperaceae pollen concentration covering the Brunhes Chron using the
- 5 algorithm of REDFIT [Schulz & Mudelsee 2002] from the statistical package PAST version 3.14 (1999-
- 6 2006) [Hammer et al. 2001]. The E-Heathland and Cyperaceae curves each consisted of 181 data
- 7 points between 0 and 790 ka. REDFIT was run with 2 times oversampling, a Blackman-Harris window,
- 8 and 2 overlapping averaging segments resulting in a bandwidth of 0.004291; false alarm level was
- 9 99.17. The ln(Fe/Ca) curve contained 2307 data points between 1 and 790 ka. REDFIT was run with 2
- 10 times oversampling, a Blackman-Harris window, and 3 overlapping averaging segments resulting in a
- 11 bandwidth of 0.005726; false alarm level was 99.91. The figure shows the power of ln(Fe/Ca) ratios
- 12 (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
- ballowidth for each spectrum and a parametric approximation of the level above the hum hypothesis
- 15 of a red noise model using X^2 -test at 90% (dashed lines). Grey bars indicate the orbital periodicities of
- 16 100, 41, 23, and 19 ka). Note the maximum in spectral density at 23 ka (precession) in the power
- 17 spectrum of ln(Fe/Ca) and the lack of spectral density at the precession bands (23 and 19 ka) in the
- 18 power spectrum of the E-Heathland values. The Cyperaceae pollen concentration, which is both
- 19 influenced by the expansion of Cyperaceae (sedges) and by the transport of pollen by river discharge,
- 20 shows significant power at both the 100 and 19 ka.
- 21



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23 Supplementary References

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- 1 Excel-Tables
- Supplementary Table 1: Family, Pollen taxon, group, growth form, endmember assemblage of
 maximum score.
- 4 Supplementay Table 2: Family, Pollen taxon, group, growth form, score per endmember (E-
- 5 Mountain-Forest, E-Heathland, E-Woodland, E-Shrubland), significance of taxon scores (r²) for two
- 6 endmember analyses [this study and Dupont et al. 2011].
- 7 Supplementary Figures 1-4

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9

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, <u>Lisiecki &</u>

13 <u>Raymo 2005</u>].





2 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 foraminifers of Core MD96-2048 (violet line) and of global stack LR04 (black line, <u>Lisiecki</u>

4 Stable oxygen is 5 <u>& Raymo 2005</u>].



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2 Supplementary Figure 3. Endmember assemblage scores and selected pollen taxa for E-Shrubland (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 & Daving 2005)

5 <u>Raymo 2005</u>].



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2 Supplementary Figure 4. Endmember assemblage scores and selected pollen taxa for E-Woodland (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, <u>Lisiecki &</u>

5 <u>Raymo 2005</u>].