Response to reviewers' comments – manuscript cp-2014-152

Response to Prof. Henry Hooghiemstra's comments

page 1: I have noted the first introductions of acronyms and Figures. It shows that Suppl. Fig. 4 apparently does not exist and re-numbering is required. By the way, I have not seen any of the Supplementary intomation, figures and tables as they were not included in the files I have downloaded.
28: The acronym 'BUS' has not been explained. Notwithstanding, I guess I have understood the text.
We have double checked all acronyms and made sure that they are defined when they first appear in the text. Fig. S4 does exist and we have checked that each Figure is cited where appropriate.

Most acronyms introduced in the Abstract do not repeat in the Abstract text and can be omitted.
We have omitted unnecessary acronyms in the Abstract

87: Another relevant comparison of terrestrial and marine pollen spectra, and an analysis how well marine pollen spectra do reflect vegetation distributions on the adjacent continent is Lézine & Hooghiemstra 1990.
We have now included this paper to the list of works on pollen-vegetation relationships along the African margin

112: It is always tricky to identify who was the first. Although Goldblatt's (1978) paper differs in scope to White (1983), Goldblatt produced with his paper an impressive understanding the biomes in southern Africa and this paper is worth mentioning.
We have reviewed and cited the paper by Goldblatt. The sentence was also rephrased to account for this change.

Fig. 1c & related text: A 'Mean Annual Precipitation'map is useful for most parts of the world. However, for southwestern Africa in particular the Mean Annual Precipitation is extremely negative and the water deficit (precipitation minus evaporation) amounts between -1700 to -3800 mm/yr (see maps on p. 17 and 18 in Barnard (ed.) 1998). Thus, the legend in Fig. 1c "Low = 0" serves better the records of meteorological stations than the understanding of vegetation distribution.
For example Lüderlitz with a coastal location has a water deficit of -2600 to -2400 mm/yr whereas inland-located Keetmanshoop a water deficit of -3800 to -3600 mm/yr ! So all numbers are dramatically far from zero, making the current map almost 'incorrect' for the aim of this paper: for example, the present Fig. 1c suggests that the moisture gra- dient (plant available moisture) between both cities is in opposite direction. Therefore, adding a Water Deficit Map as Fig. 1d would be helpful to show the climatic constraints of biome distribution in southwestern Africa. As far as I see, such map would not lead to new arguments in reasoning and conclusions will not change.

We have now included a Water deficit map in Figure 1 based on Barnard (1998) and data from the Digital Atlas of Namibia (www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia). We also added a note about water deficit in the desert biome.

231 and 184/185: information about the pollen sum is contradictory and needs attention.
One sentence refers to the pollen sum in the terrestrial surface samples, while the other sentence refers to the pollen sum in the marine sediment samples. Clarification has been added.

Fig. 3: A technical issue: it takes some time to realise that the blue-hatched area is a continuation of the blue area. My suggestion is to fill the hatched area for ~ 80% with blue colour (instead of 50%) in order to show more clearly we a dealing with one unit of which the data originate from two different studies.
We modified the figure and increased the hatching density in the blue polygons

Response to reviewers' comments – manuscript cp-2014-152

Response to Dr Charlotte S. Miller's comments

Page 346 Line 3 – add ka after 24
We eliminated this acronym from the abstract following the suggestion from Prof. Hooghiemstra.

Line 14 – suggest, not suggested?
We prefer "suggested" to keep the same tense throughout the Abstract

Line 25 – you mention how the strength in the BUS is linked to arid conditions and the extent of the coastal Namib Desert. Do you mean that increased strength in the BUS results in increased aridity and an increase in the extent of the desert? Does the coastal desert expand inland? Maybe just make it a little clearer.
We have rephrased the sentence and eliminated the reference to the desert as the paragraph is about climate. It now reads: "The Benguela Upwelling System (BUS) also affects climate in southwestern Africa and is linked to arid conditions on the continent (Lutjerharms and Meeuwis, 1987)".
We make the point about the link between low precipitation in the desert and BUS in the Modern environmental setting section.

Page 347 Line 3 – significant yes, as well as incredibly complex.
We have rephrased the sentence to acknowledge the complexity of the system. Now it reads "The complex link between globally-important atmospheric and oceanic systems and the climate of southern Africa make understanding past climate change in the region particularly significant".

Line 5 – markers? Biomarkers? Do you mean proxies?
We have replaced "markers" with "planktic foraminifera assemblages" to add precision.

Line 25 – Walker – capital letter
Corrected

Page 348 Line 4 – not just today, and important in the face of future climate change scenarios surely? Maybe you could give an indication of what these scenarios suggest for southern Africa in the future? Is it likely here that the climate will become drier?
We have rephrased the sentence, it now reads: "Whether the last interglacial was characterised by orbitally-driven increased aridity or increased precipitation may have significant implications for resource availability and climate in the region today and in the near future. Projected patterns of precipitation change for the end of the 21st century indicate at least a 20% reduction of precipitation in southern Africa compared to pre-2005 values (IPCC, 2014). Understanding glacial-interglacial

climate and vegetation dynamics in this region may help unravel how much of the projected precipitation change corresponds natural variability".

Page 351 Line 18 – is all the calcium carbonate from foraminifera?
To avoid overstating the information, we have modified the phrase and eliminated the reference to foraminifera: "The sediments of this 32-m long core were composed of calcium carbonates, biogenic silica, clays and organic matter (Bertrand et al, 1996)".

Page 352 Line 1 – check tense – eliminated, and concentrated
We have replaced the word "eliminated" with "separated"

Page 353 Line 3 – did you do the DCA analysis on all fossil pollen taxa, or those with their % above a certain threshold? Did you try doing the DCA of the individual samples (sample scores)?
We run DCA analysis on the complete dataset and also filtering rare taxa. We have added this information and a reason for preferring the DCA where we filtered rare taxa: "These ordinations were performed on the complete dataset and filtering out pollen morphotypes that only occurred only in one sample. Results from the ordination performed on the reduced dataset were preferred when differences in axis scores were not discernible to reduce the effect of rare taxa".
Any clustering in sample scores may indicate different vegetation compositions of the individual MISes?
We observed no clustering of samples, and have now included a sentence in the Results about this: "DCA1 axis scores from MIS 5 and 3 are overall positive in value, while scores from MIS 6 and 4 are negative, although clustering of samples was not observed."

Line 28 – can you give an average sedimentation rate for the core?
We have calculated and added the average sedimentation rate

Line 28 – Can you show an age-depth model in the sup material?
We have added an age-depth curve as panel b in Supplementary Figure 1.

Page 354 Line 7 – how many taxa were identified in all the samples? How many unknowns?
We have added the requested information: "We identified 83 different pollen taxa in the whole sequence, and the mean number of pollen taxa per sample was 21. The proportion of unknown pollen taxa was between 1% and 2% per sample".

Line 13 – why would low primary productivity result in low pollen concentrations? Unclear.
We have added a sentence to clarify: "The low net primary productivity that characterizes the vegetation of southwestern Africa (Imhoff et al 2004) is probably

linked to low pollen production and could explain relatively low pollen concentrations in the continental margin (Supplementary Fig.2).".

Page 357 Line 21 – where is the DCA plot? Tell us that it is in the supplementary material. Can you give an indication of what DCA axis 1 actually represents?
The DCA axis 1 scores are plotted in Figure 4 as indicated at the beginning of the paragraph. To add clarity, we have added a few sentences: "The axis scores on DCA1 reveal changes in the composition of pollen assemblages that also resemble variations in the $d^{18}O_{benthic}$ record (Fig.4). This similarity suggests that glacial-interglacial vegetation changes in southern Africa track global ice volume changes. DCA1 axis scores from MIS 5 and 3 are overall positive in value, while scores from MIS 6 and 4 are negative, although clustering of samples was not observed. The DCA1 axis represents relative changes in the pollen assemblage from one sample to the next".

Page 358 Line 5 – Does Fig. S2 have anything to do with core top samples? I think that is the complete pollen record? Is the link to the figure is in the wrong place?
This was a mistake. Fig. 4 is now cited istead of Fig. S2.

Page 359 Line 15 – nss? Define.
$nssCa^{2+}$ refers to sea-salt calcium flux. This is now defined.

Page 362 Line 11 – why is there an increase in both the amplitude and frequency of shifts between positive and negative DCA from 100 ka onwards? What does the DCA axis 1 actually represent? You mention possibly enhanced trade wind variability, but I guess if so then this is not related to orbital cyclicity (from 100 ka onwards the amplitude of the precessional variability decreases). Any idea why trade wind variability increased?
The DCA1 Axis scores reflect the changes in the pollen assemblage (this is explained in the manuscript more clearly following the reviewer's suggestion). In this section we explain that the record of pollen taxa like Restionaceae in MD96-2098 seem to support previous work where other authors have suggested increased trade wind strength, but we would prefer not to speculate on why the millennial-scale trade wind variability may have increased during the last 100 ka. We have added more detail to the paragraph to clarify some of the questions and referred the reader to the supplementary material where this point is discussed: "Increased Restionaceae pollen could indicate expansions of Fynbos vegetation, or enhanced pollen transport from the Fynbos region linked to increased trade-wind strength (see additional discussion on Present-day pollen-vegetation-climate relationships in the Supplementary material). Other Fynbos indicators did not display the same trend (Fig. 4), suggesting that Restionaceae variability between 100 ka and 24 ka were more likely the result of enhanced variability of southeast trade winds.

Figure comments: Fig 4 – not sure if a dashed line every 10 ka is necessary. It makes it difficult to see the stage boundaries. You don't need the references on the actual figure if you mention them in the figure caption. Add some arrows of interpretation

on your data (like you have done with the 3 proxy records at the bottom of the figure).
We have eliminated the lines and moved references to the Figure caption. We also added arrows for the interpretation of our data in panel (b).

Sup. fig 1. caption – remove brackets around references Sup. fig. 2 – italicize sp. and genus where necessary.
Corrected.

Increased aridity in southwestern Africa during the warmest periods of the last interglacial

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Abstract

Terrestrial and marine climatic tracers from marine core MD96-2098 were used to reconstruct glacial-interglacial climate variability in southwestern Africa between 194 and 24 thousand years before present. The pollen record documented three pronounced expansions of Nama-Karoo and fine-leaved savanna during the last interglacial (Marine Isotopic Stage 5 – MIS 5). These Nama-Karoo and fine-leaved savanna expansions were linked to increased aridity during the three warmest substadials of MIS 5. Enhanced aridity potentially resulted from a combination of reduced Benguela Upwelling, expanded subtropical high-pressure cells, and reduced austral-summer precipitation due to a northward shift of the Intertropical Convergence Zone. Decreased austral-winter precipitation was likely linked to a southern displacement of the westerlies. In contrast, during glacial isotopic stages MIS 6, 4 and 3, Fynbos expanded at the expense of Nama-Karoo and fine-leaved savanna indicating a relative increase in precipitation probably concentrated during the austral winter months. Our record also suggested that warm-cold or cold-warm transitions between isotopic stages and substages were punctuated by short increases in humidity. Increased aridity during MIS 5e, 5c and 5a warm substages coincided with minima in both precessional index and global ice volume. On the other hand, austral-winter precipitation increases were associated with precession maxima at the time of well-developed northern-hemisphere ice caps.

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Key words

Benguela upwelling, fine-leaved savanna, Intertropical Convergence Zone (ITCZ), last interglacial, Nama-Karoo, southern westerlies, southwestern Africa.

1. Introduction

Southern Africa is influenced at present by tropical and subtropical atmospheric circulation and by both the Indian and the Atlantic Oceans (Tyson and Preston-Whyte, 2000). The water exchange between the two oceans is termed the Agulhas leakage and is suggested as a potential trigger of meridional overturning circulation changes (Beal et al., 2011; Biastoch et al., 2008). The Benguela Upwelling System (BUS) also affects climate in southwestern Africa and is linked to arid conditions on the continent (Lutjeharms and Meeuwis, 1987). The complex link between globally-important atmospheric and oceanic systems and the climate of southern Africa make understanding past climate change in the region particularly significant.

Whether southern Africa was characterised by aridity or by increased humidity during the last interglacial remains unclear. Previous work using planktic foraminifera assemblages has documented an intensification of the Agulhas leakage during interglacials (Peeters et al., 2004), which suggests a reduced influence of the subtropical front and reduced precipitation. Other works have shown increased sea surface temperatures (SST) in the Benguela Current during interglacials linked to weakening of BUS (Kirst et al., 1999). Additionally, decreased influence of the Intertropical convergence zone (ITCZ) has been suggested for southern Africa during interglacials (Tyson, 1999) pointing to its northward migration. These three climatic factors combined would result in a slight increase in humidity in northeastern South Africa during interglacials. However, other works suggest contrasting climate conditions with increased interglacial aridity based on ratios of aeolian dust and fluvial mud in marine sediments off southern Africa (Stuut and Lamy, 2004).

Vegetation-based climate reconstructions for southern Africa have been less straight forward given the paucity of records (Dupont, 2011) and fragmentary nature of some terrestrial sequences (Scott et al., 2012; Meadows et al., 2010). On one hand, some records point to expansions of the Fynbos biome (Shi et al., 2001) and the winter-rainfall zone during glacial periods (Chase and Meadows, 2007), and to a contracting Namibian Desert during interglacials (Shi et al., 2000) and the late Holocene (Scott et al., 2012). On the other hand, it has been suggested that savannas expanded southwards during the Holocene climate optimum (Dupont, 2011), and that the

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southern Africa summer-rainfall zone expanded during interglacials due to a strengthening of the Walker circulation and a southward migration of the ITCZ (Tyson, 1999). Contrastingly, significant reductions of austral-summer precipitation in southern Africa are suggested to coincide with precession minima both during glacials and interglacials (Partridge et al., 1997), and are independently supported by reductions of grass-fuelled fires in the subcontinent (Daniau et al., 2013). The latter observations suggest aridity increase and savanna biome reductions, instead of expansions, during the last interglacial precession minima. Whether the last interglacial was characterised by orbitally-driven increased aridity or increased precipitation may have significant implications for resource availability and climate in the region today and in the near future. Projected patterns of precipitation change for the end of the 21st century indicate at least a 20% reduction of precipitation in southern Africa compared to pre-2005 values (IPCC, 2014). Understanding glacial-interglacial climate and vegetation dynamics in this region may help unravel how much of the projected precipitation change corresponds natural variability.

In this study we aim to disentangle the contrasting hypotheses of orbital-scale climate change in southern Africa by combining terrestrial and marine tracers from the marine sequence MD96-2098. We use pollen and charcoal as terrestrial tracers, and $\delta^{18}O$ from benthic foraminifera as a marine tracer. Vegetation reconstructions from marine records have contributed to our understanding of ocean-land interactions in many regions of the world, including the Iberian Peninsula (Sánchez Goñi et al., 2000), the eastern subtropical Pacific (Lyle et al., 2012), and the tropical Atlantic (González and Dupont, 2009). Studies from the African margin (e.g. Dupont (2011); Dupont and Behling (2006); Hooghiemstra et al. (1992); Leroy and Dupont (1994); Lézine and Hooghiemstra (1990)) have demonstrated that pollen records from marine sequences are reliable and useful tools to reconstruct changes in the regional vegetation of adjacent landmasses and the climate dynamics at orbital and suborbital timescales. In arid environments, marine sequences are particularly essential in providing continuous records of vegetation change at the regional scale.

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The pollen sequence from MD96-2098 presented here covers the period between 24 and 190 thousand years before present (ka) and provides an integrated picture of past regional vegetation changes in southwestern Africa. Southwestern Africa refers here to the western half of South Africa and Namibia that is drained by the Orange River. We compare vegetation-based atmospheric changes with independent climatic markers from the same marine sequence, along with other regional records for oceanic conditions and global ice dynamics, to reconstruct atmospheric and oceanic configurations around southern Africa for MIS 6, 5, 4 and 3.

2. Modern environmental setting

The southwestern part of the African continent (Atlantic side) is influenced by the seasonal migration of the subtropical front and the southern westerlies that bring precipitation during the austral-winter months (Beal et al., 2011). Precipitation in southwestern Africa is additionally controlled by the cold Benguela current and wind-driven upwelling that results in aridity on the adjacent continent (Stuut and Lamy, 2004). In the Indian Ocean, warm waters from the Agulhas current (Beal and Bryden, 1999) and austral-summer heat enhance evaporation and result in relatively high precipitation in southeastern Africa and the interior of the continent (Fig.1). Austral-summer precipitation is also linked to the position of tropical low pressure systems (e.g. ITCZ) and reduced subtropical high pressure (Tyson and Preston-Whyte, 2000). As tropical low-pressure systems migrate northwards during the austral winter, subtropical high pressure significantly reduces austral-summer precipitation in southern Africa. This climatic configuration broadly determines the vegetation distribution in southern Africa.

The vegetation of southern Africa was initially classified into phytogeographical regions (White, 1983; Goldblatt, 1978), and later revisited and described into seven biome units (Rutherford, 1997). These include the Succulent-Karoo, Nama-Karoo, Desert, savanna, Fynbos, Grassland, and forest (Fig.1). The Succulent-Karoo receives between 20 and 290 mm/yr of which more than 40% falls during the austral-winter months (Rutherford, 1997). The two most abundant succulent families

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are Crassulaceae and Mesembryanthemaceae, and non-succulents are Anacardiaceae, Asteraceae, and Fabaceae (Milton et al., 1997). C4 perennial grasses (Poaceae) have relatively low abundance in the Succulent-Karoo (Milton et al., 1997).

The Nama-Karoo receives precipitation from 60 to 400 mm/yr falling primarily during the austral summer (Palmer and Hoffman, 1997). Vegetation is characterized as dwarf open shrubland with high abundance of Poaceae, Asteraceae, Aizoaceae, Mesembryanthemacae, Liliaceae and Scrophulariaceae (Palmer and Hoffman, 1997). Grasses from the Poaceae family can be particularly dominant in the Nama-Karoo biome (Fig.2a). The Nama- and Succulent-Karoo are structurally similar but influenced by different seasonal precipitation (Rutherford, 1997). The Nama-Karoo is influenced primarily by austral summer precipitation, while the distribution of the Succulent-Karoo coincides with the austral-winter rainfall region (Chase and Meadows, 2007). To the northwest, the Nama-Karoo biome transitions into the Desert, where mean annual precipitation can be as low as 20 mm/yr (Jürgens et al., 1997) and water deficit as high as 2000 mm (Barnard 1998, Fig.1d). The Desert reaches 300 km inland and its low precipitation input is linked to the intensity of BUS (Cowling et al., 1994).

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High precipitation seasonality (i.e. difference between dry-season and rainy-season precipitation) and high austral-summer rainfall characterize the savanna. The savanna biome represents a mosaic that includes shrublands, dry forests, lightly-wooded grasslands, and deciduous woodlands (Scholes, 1997). At the landscape scale however, the savanna can be subdivided into the fine- and broad-leaved savannas based on moisture conditions and soils (Scholes, 1997). The fine-leaved savanna (Fn-LSav) is found in dry and fertile environments (between 400 and 800 mm/yr), and the broad-leaved savanna (Bd-LSav) is found in nutrient-poor and moist environments (up to 1500 mm/yr) (Scholes, 1997). Additionally, in the Fn-LSav fuel load and fire frequency are very low, while Bd-LSav has high fuel load and fire frequency (Scholes, 1997; Archibald et al., 2010). The Fn-LSav is found to the northeast of the Nama-Karoo biome (Fig.1), known as the Kalahari Highveld transition zone (Cowling and Hilton-Taylor, 2009). Due to the transitional character of the Fn-LSav, some of its outer parts have been classified as grassland or Nama-Karoo (White, 1983). The composition of the Fn-LSav can be similar to that of the Nama-Karoo, with dominance of C4 grasses (Poaceae) and succulent plants, but it differs in having scattered trees (Fig.2b) (Cowling et al., 1994). The Bd-LSav is characterized by broad-leaved trees from the Caesalpinaceae and Combretaceae families and an understory dominated by grasses (Scholes, 1997).

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The grassland biome is dominated by C4 grasses and non-grassy forbs as *Anthospermum* sp., *Lycium* sp., *Solanum* sp. and *Pentzia* sp. (O'Connor and Bredenkamp, 1997). At the high elevations the biome is dominated by C3 grasses. In the grasslands, precipitation is highly seasonal with mean annual rainfall ranging between 750 and over 1200 mm, falling primarily during the austral-summer months (O'Connor and Bredenkamp, 1997) (Fig.1).

The southernmost part of Africa is characterised by the Fynbos biome, a fire-prone vegetation dominated by Ericaceous and Asteraceae shrubs, diverse *Protea* shrubs and trees, and Restionaceae herbs (Cowling et al., 1997a). The Fynbos biome receives relatively high annual precipitation (1200 mm per year) concentrated during the austral-winter months (Rutherford, 1997). The coastal forest biome is found along the eastern coast of the subcontinent and often occurs in small patches with high abundance of *Podocarpus* (Rutherford, 1997). *Podocarpus* patches can also be found in the southeastern part of the Fynbos.

3. Materials and Methods

3.1 Marine core description and pollen analysis

Pollen analysis was conducted on marine core MD96-2098 (25°36'S, 12°38'E). This giant CALYPSO core was collected during the IMAGES II-NAUSICAA cruise at a 2910-m water depth from the Lüderitz slope in the Walvis Basin, approximately 500 km northwest of the Orange River mouth (Fig.1). The sediments of this 32-m long core were composed of calcium carbonates, biogenic silica, clays and organic matter (Bertrand et al., 1996). The core was sampled every 10 cm between 450

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and 1940 cm (uncorrected depth) for pollen analysis. The uncorrected depth did not take into account artificial gaps created during piston extraction (Bertrand et al., 1996).

Sample volumes were estimated by water displacement. Pollen concentrations per unit volume were calculated based on a known spike of exotic *Lycopodium* spores added to each sample. Pollen extraction techniques included treatment with Hydrofluoric and Hydrochloric acids, and sieving through 150 and 10-µm filters. This filtration allowed separating small non-palynomorph particles and concentrating pollen grains and spores. An independent test of this protocol showed that the use of a 10-µm sieve had no effect on the pollen spectra of marine samples, i.e. comparison of filtered and unfiltered sample counts showed that taxa were not selectively filtered out during pollen preparation and concentration (see http://www.ephe-paleoclimat.com/ephe/Lab%20Facilities.htm for a detailed pollen preparation protocol). Marine sediment samples from MD96-2098 were analysed under the microscope until a sum of at least 100 pollen grains excluding fern spores was reached.

We used the pollen spectra from 31 terrestrial surface samples collected along a transect (Fig.1) from Cape Town (South Africa) to Lüderitz (Namibia) and designed to cover the four major biomes of southwestern Africa (Table S1). The transect included samples from the Desert, Fynbos, Nama- and Succulent-Karoo. The terrestrial surface samples were treated with standard acetolysis (Faegri and Iversen, 1989) and analysed under the microscope until a pollen sum greater than 300 grains was reached. Additional details on terrestrial surface-sample collection and analysis can be found in the Supplementary material. We also used previously-published pollen spectra from 150 additional surface samples collected between 22° and 35° latitude south (APD, Gajewski et al. 2002). These pollen spectra were used to assess the distribution of Poaceae pollen abundance and other pollen taxa with potential indicator value for large biomes in southern Africa. ArcGIS 10 was used to draw iso-lines of pollen percentages by interpolating values from a total of 178 surface samples through the natural neighbour method. Additionally, we analysed two marine pollen samples from the upper part of core MD96-2098 (at 5 and 10 cm depth). We compared the pollen spectra from

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these core top samples with the pollen signal of the modern vegetation to evaluate how well marine sediments represent the vegetation of the adjacent landmasses, and to aid interpretation of the pollen record (see also Lézine and Hooghiemstra 1990).

Pollen identification was aided by the pollen reference collection of the Department of Plant Sciences at University of the Free State (Bloemfontein, South Africa), the African Pollen Database (APD) (http://medias3.mediasfrance.org/pollen), the Universal Pollen Collection (http://www.palyno.org/pollen), and pollen descriptions published by Scott (1982). Pollen grains from the Asteraceae family were grouped into three pollen taxa: *Artemisia-type*, *Stoebe*-type and other morphotypes were classified into Asteraceae-other. Some morphotypes were grouped into family types: Acanthaceae, Chenopodiaceae-Amaranthaceae, Crassulaceae, Cyperaceae, Ericaceae, Myrtaceae, Ranunculaceae, Restionaceae, and Solanaceae.

Detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMDS) (McCune and Grace, 2002) were used as parametric and non-parametric ordinations to summarize changes in the fossil pollen record. Results from the DCA ordination were preferred when NMDS was unable to reach a stable solution after several random starts, and when stress levels were too high to allow a meaningful interpretation (McCune and Grace, 2002). These ordinations were performed on the complete dataset and filtering out pollen morphotypes that occurred only in one sample. Results from the ordination performed on the reduced dataset were preferred when differences in axis scores were not discernible between the two ordinations to reduce the statistical effect of rare taxa.

3.2 Marine core chronology

Two sediment gaps between 693 and 709 cm and 759 and 908 cm were described in the core log. These gaps were considered artificial and linked to piston extraction (Bertrand et al., 1996), thus the record could be assumed continuous. Depths were corrected to take into account these artificial sediment gaps. An age model was established for the record based on 16 marine isotope

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events (MIE) from the *Cibicidoides wuellerstorfi* $\delta^{18}O$ benthic record of MD96-2098 (Bertrand et al., 2002) and 14 Accelerator Mass Spectrometer radiocarbon ages (AMS ^{14}C) from mixed planktonic foraminifera extracted from MD96-2098 (Table S2). The 14 AMS ^{14}C dates were produced at the Laboratoire de Mesure du Carbone 14. One single ^{14}C date showed an age reversal and was therefore excluded from the chronology on the principle of parsimony. AMS ^{14}C ages were calibrated using the marine09.14c curve (Hughen et al., 2004) from CALIB REV5.0 (Reimer et al., 2013). We applied a 400-year global reservoir correction factor and a weighted mean Delta R of 157 years derived from 9 regional reservoir error values from the Marine Reservoir Correction Dataset (Dewar et al., 2012; Southon et al., 2002). MIE ages were derived from LR04 global stack (Lisiecki and Raymo, 2005) and additional sources (Henderson and Slowey, 2000; Drysdale et al., 2007; Waelbroeck et al., 2008; Masson-Delmotte et al., 2010; Sánchez Goñi and Harrison, 2010) (Fig. S1). Sample ages were calculated using a linear interpolation between AMS ^{14}C ages and MIE using the R package PaleoMAS (Correa-Metrio et al., 2010). The average sedimentation rate of core MD96-2098 amounts to 0.01 cm yr^{-1}.

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4. Results and discussion

4.1 Pollen preservation and sources in marine core MD96-2098

Pollen sums ranged from 100 to 240 grains (excluding fern spores) in the 141 samples analysed from core MD96-2098. We identified 83 different pollen taxa in the whole sequence, and the mean number of pollen taxa per sample was 21. The proportion of unknown pollen taxa was between 1% and 2% per sample. The total pollen concentration ranged between ca. 300 and 16,000 grains/cm^3 during most of MIS 6, 5 and 3 and increased up to 48,000 grains/cm^3 during MIS 4 (Fig. S2). The MIS 5 pollen concentrations were comparable to those found in other oceanic margins (Sánchez Goñi et al., 1999), even though BUS facilitates preservation of pollen grains and other organic microfossils at this site (Bertrand et al., 2003). The low net primary productivity that characterizes the vegetation of southwestern Africa (Imhoff et al., 2004) is probably linked to low

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pollen production and could explain relatively low pollen concentrations in the continental margin (Fig. S2).

Pollen grains are part of the fine sediment fraction and can be transported by two main vectors: aeolian or fluvial (Hooghiemstra et al., 1986; Heusser and Balsam, 1977). Dupont and Wyputta (2003) modelled present-day wind trajectories for marine core locations between 6 and 30°S along the coastline of southern Africa. They suggest aeolian pollen input to the Walvis area (23°S) via the southeast trade winds during austral summer, and dominant east-to-west wind directions during the austral fall and winter. These winds transport pollen and other terrestrial particles from the Namib Desert, southern Namibia and western South Africa. The direction of the winds indicate that the Namib Desert, Nama-Karoo and Succulent-Karoo are the most likely sources of pollen in the Walvis Bay area (Dupont and Wyputta, 2003). The authors also infer that south of 25°S wind directions are predominantly west to east and aeolian terrestrial input very low. Marine site MD96-2098 is located less than a degree south of the area determined by Dupont and Wyputta (2003) to be dominated by wind-transported terrestrial input. However, given that this threshold was established using only two marine sites located 6° apart at 23°26′ (GeoB1710-3) and 29°27′ (GeoB1722-1), it is difficult to conclude that MD96-2098 only receives wind-transported pollen.

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MD96-2098 likely receives fine sediments from the Orange River plume. Sedimentological analyses of the Orange River delta and plume indicate that fine muds are transported both northwards and southwards (Rogers and Rau, 2006). Additionally, an analysis of the imprint of terrigenous input in Atlantic surface sediments found relatively high Fe/K values along the Namibian and South African margin that could reflect the input of Orange River material (Govin et al., 2012). Pollen grains are hence likely to reach the coring site from the Orange River catchment area.

Scott et al. (2004) argue that pollen in marine sediments can be the result of long-distance transport by ocean currents, suggesting that pollen assemblages in marine sediments do not reflect accurately past changes in vegetation and climate. However, the highest pollen influx in marine sediments along this margin is near the coast and the vegetation source (Dupont et al., 2007), not along the paths of oceanic currents (i.e. Benguela Current). Additionally, analyses of pollen transport vs. source in northwestern Africa show that pollen grains can sink rapidly in the water column (Hooghiemstra et al., 1986) before they can be carried away by ocean currents. As a result, influence of oceanic currents on the composition of pollen assemblages is probably negligible. Overall, the marine site MD96-2098 might receive both aeolian and fluvial pollen input from the vegetation located east and southeast to the site.

The pollen spectra of the two core-top samples from core MD96-2098 are dominated by Poaceae (30 and 40%), Cyperaceae (20%) and Chenopodiaceae-Amaranthaceae (20 and 30%) (Fig. S2). This composition corresponds well with the pollen spectra from the three major biomes occupying today the adjacent landmasses (Fig.1a): Desert, Nama-Karoo and Fn-LSav (Fig. S3). Pollen percentages from Fynbos taxa are less than 10%, *Podocarpus* is weakly represented, and taxa specifically found in the broad-leaved savanna (e.g. Caesalpinaceae, Combretaceae) are not recorded. These results support the assumption that the main pollen source for marine core MD96-2098 is the vegetation from southwestern Africa.

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4.2 Distribution and interpretation of Poaceae pollen in terrestrial and marine surface samples

Occurrence of Poaceae pollen in all surface samples corresponds to the presence of grass species in virtually all southern African biomes (Cowling et al., 1997b). Altogether, the spatial distribution of Poaceae pollen percentages appears to be essential information to distinguish the pollen signal from major biomes, and therefore climatic zones, in this region. In the eastern and northeastern part of southern Africa, the highest percentages of Poaceae pollen (up to 90%) are found in the pollen rain of the Bd-LSav and grasslands. In the western half of southern Africa, Poaceae pollen percentages in terrestrial surface samples are up to 60% in the Nama-Karoo and its transition with the Fn-LSav (Fig.3). This suggests an overrepresentation of Poaceae in the pollen rain of the Nama-Karoo biome where grasses can be abundant but are not necessarily dominant.

Poaceae is likely to be well represented in other parts of the Fn-LSav, but the paucity of surface samples from this biome hinder drawing further conclusions. In the Namib Desert where the proportion of grasses in the vegetation is low, Poaceae pollen percentages are as high as 25% in terrestrial surface samples, comparable to 20% reported from hyrax dung (Scott et al., 2004).

In marine surface samples along the southwestern African coast, Poaceae pollen percentages are as low as 10% in samples collected offshore the Bd-LSav at around 15°S (Fig.3). Poaceae pollen percentages increase to the south and the highest values (40%) are found between 20 and 25°S (Dupont and Wyputta, 2003) and correspond well with the distribution of the Desert and the Fn-LSav on the continent. The Poaceae pollen percentages in the two core-top samples from MD96-2098 are used to extend the iso-lines drawn by Dupont and Wyputta (2003) to 25.5°S, and show that Poaceae pollen percentages are between 30 and 40% offshore the Desert, Nama-Karoo and Fn-LSav biomes. As Poaceae pollen percentages in Desert surface samples are less than 25%, high percentages of grass pollen from marine sediments in the southwestern Africa margin should be interpreted as indicator of the Nama-Karoo and the Fn-LSav, where Poaceae is as high as 70% in terrestrial surface samples. Our field observations also support this view as we found large grass-dominated vegetation in the Nama-Karoo and Fn-LSav (Fig. 2).

4.3 Southwestern Africa vegetation and climatic changes from MIS 6 to 2

The pollen record presented here spans from 24.7 to 190 ka. A log transformation of concentration values in MD96-2098 results in a curve remarkably similar to that of $\delta^{18}O_{benthic}$ values (Fig.4) and may be linked to changes in pollen input at the coring site. Relative increases in pollen concentration could indicate an increase in pollen supply during low sea-level stands when the vegetation source was closest (i.e. during glacial stages). However, this is unlikely because of the rapid depth change in a few kilometres of the Walvis continental shelf. An increase of pollen concentration might indicate instead an increase in pollen supply during glacials, and/or an increase in pollen preservation linked to upwelling enhancement as suggested by Pichevin et al. (2005).

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Glacial-interglacial pollen concentration variations have no effect on the interpretation of the pollen record which is based on relative frequencies, but they do indicate the influence of the obliquity signal in the pollen record from MD96-2098. In other words, the effect of orbital-scale precipitation changes on the density of the vegetation and the pollen production as a consequence.

The axis scores on DCA1 reveal changes in the composition of pollen assemblages that also resemble variations in the $\delta^{18}O_{benthic}$ record (Fig.4). This similarity suggests that glacial-interglacial vegetation changes in southern Africa track global ice volume changes. DCA1 axis scores from MIS 5 and 3 are overall positive in value, while scores from MIS 6 and 4 are negative, although clustering of samples was not observed. The DCA1 axis represents relative changes in the pollen assemblage from one sample to the next. A series of large-magnitude changes in DCA1 axis scores are also visible and increase in amplitude after c. 100 ka. Such changes in DCA Axis1 scores are also observed during MIS 6 but are of lesser magnitude. Changes in DCA axis scores suggest significant changes in vegetation composition from one sample to the next.

Nama-Karoo and Fn-LSav pollen percentages are up to 60% during MIS 5 and display three percentage peaks that correspond with $\delta^{18}O_{benthic}$ and precession minima (Fig.4a). These percentage peaks are centred at 125 ka, 107 and 83 ka. The pollen spectra from warm marine substages MIS 5e, 5c and 5a is comparable to the core-top samples (Fig. 4) and corresponds well with the modern pollen spectra from Nama-Karoo and Fn-LSav (Fig. S3). Additionally, Nama-Karoo and Fn-LSav pollen percentages in the core-top samples are relatively low compared to their maximum during MIS 5e (Fig.4b).

During MIS 6 and 4, Nama-Karoo and Fn-LSav percentages are reduced and co-vary with $\delta^{18}O_{benthic}$ values. Pollen percentages of Chenopodiaceae-Amaranthaceae and Asteraceae-other are relatively high and increase along with enriched $\delta^{18}O_{benthic}$ values during MIS 6 and at the end of MIS 4 (Fig. S2). Cyperaceae pollen percentages vary throughout the record and are as high as 40% during MIS 4 (Fig. S2). Fynbos indicators (Ericaceae, *Passerina*, *Anthospermum*, *Cliffortia*, and *Protea* *Artemisa*-type and *Stoebe*-type) show relative increases in pollen percentage during MIS 6, 4 and 3

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(Fig.4b and Fig. S2). Pollen percentages of Restionaceae increase after the 105-ka $\delta^{18}O_{benthic}$ minimum and remain abundant during the rest of MIS 5 through MIS 3, despite a relative decrease during MIS 4. *Podocarpus* percentages are lower than 10% but show increases at stage boundaries around 135 ka (MIS 6/5), 100 ka (5c/5b), 75 ka (MIS 5a/4), 60 ka (MIS 4/3), and around 27 ka (MIS 3/2) (Fig. S2).

The increases of Nama-Karoo and Fn-LSav during MIS 5e, 5c and 5a suggest an increase in aridity in southwestern Africa that likely resulted from expansions in three directions (Fig. 5). The Nama-Karoo and Fn-LSav probably expanded to the northwest into the present-day area of the coastal Namib Desert as the intensity of BUS weakened during MIS 5 warm substages. This weakening has been documented through alkenone-based SST from marine core GeoB1711-3 (Kirst et al., 1999) (Fig.4c), foraminifera-assemblage based SST (Chen et al., 2002) and grain-size end-member modelling (Stuut et al., 2002). Stuut and Lamy (2004) also suggested reduced atmospheric circulation and weakening of trade winds during interglacials compared to glacials, resulting in a reduction of the wind-driven upwelling. A weakened BUS and the associated relative increase in humidity likely led to a colonization of Desert areas by Nama-Karoo or Fn-LSav (Fig.5a). Comparable contractions of the Namib Desert linked to increased SSTs and weakening of BUS during the present interglacial are documented by Shi et al. (2000).

To the south, the Nama-Karoo and Fn-LSav likely expanded at the expense of the Succulent-Karoo and Fynbos. Warm Antarctica temperatures recorded during MIS 5 substages (EPICA, 2006) would drive the southern westerlies southwards (Ruddiman, 2006), contributing to the ventilation of deep CO_2-rich waters in the southern Ocean (Toggweiler and Russell, 2008). This mechanism would explain the paralleling trends observed between MIS 5 Nama-Karoo and Fn-LSav expansions in southern Africa and the atmospheric CO_2 record (Petit et al., 1999; Bereiter et al., 2012) (Fig.5). A southward migration of the westerlies during the present interglacial, relative to their position during the previous glacial, has been suggested by Weldeab et al. (2013), and correlated with non-sea-salt calcium flux (nssCa^{2+}) from Antarctica (Röthlisberger et al., 2008). Such poleward migration

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of the westerlies during the present interglacial is equivalent to the westerlies migration we propose for warmest periods of the last interglacial. The increased Agulhas leakage documented in the Cape basin record during the last interglacial (Peeters et al., 2004) (Fig.4c) has been linked to a southward migration of the subtropical front and the westerlies, reducing austral-winter precipitation over southern Africa. Such an atmospheric configuration would in turn favour the development of the Nama-Karoo at the expense of Succulent-Karoo and Fynbos biomes (Fig.5a).

To the northeast, Nama-Karoo and Fn-LSav likely pushed the limit of Bd-LSav equatorward as austral-summer precipitation decreased (Fig.5a). Austral-summer precipitation reductions in southern Africa have been linked to reduced austral-summer insolation in the Pretoria saltpan (Partridge et al., 1997) and to reductions of grass-fuelled fires during precession minima reconstructed from MD96-2098 (Daniau et al., 2013) (Fig.4b). Increased northern-hemisphere insolation during MIS 5 warm substages would drive the ITCZ northwards while subtropical high pressure cells over the south Atlantic and the Indian Oceans would expand (Fig.5a) (Ruddiman, 2006). Such changes in the tropical and subtropical pressure systems would allow the expansion of the Nama-Karoo and Fn-LSav to the northeast.

In contrast with the results presented here, previous works report poleward interglacial expansions of savannas based on pollen records from marine sediments along the southwestern African coast (Dupont, 2011). These studies univocally interpret the Poaceae pollen percentage increases as the result of savanna expansions. Such an interpreation is potentially plausible in marine records collecting pollen from broad-leaved savanna vegetation, e.g. the Limpopo basin (Dupont, 2011). However, our results show that Poaceae pollen percentage increases in sequences located off the southwestern African coast can alternatively indicate the expansion of fine-leaved savanna and Nama-Karoo vegetation. Previous studies on the other hand do not differentiate between the Bd-LSav and Fn-LSav, despite the significant climatic and structural differences between these two types of vegetation. The Bd-LSav is influenced by fire and receives a considerable amount of precipitation during the austral summer (Scholes, 1997). The Fn-LSav is structurally and

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climatically more similar to the Nama-Karoo biome, as it receives very low austral-summer precipitation and does not burn (Archibald et al., 2010) despite being under a regime of significant precipitation seasonality (Scholes, 1997). If high Poaceae pollen percentages during MIS 5 warm substages in our record were related with expansions of the Bd-LSav and increased summer precipitation, the fire activity should also increase during these substages. Instead, an independent charcoal record from the same marine sequence MD96-2098 (Fig.4b) documents reductions of grass-fuelled fires and a decrease in austral-summer precipitation during MIS 5 precession minima (Daniau et al., 2013). An atmospheric configuration with reduced austral summer precipitation in southern Africa and the ITCZ shifted northward during the warmest periods of MIS 5 is also consistent with documented strengthening of Asian monsoon and weakening of the South American monsoon during the last-interglacial precession minima (Wang et al., 2004).

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Our results suggest that the Bd-LSav retreated equatorwards during MIS 5 precession minima, while Nama-Karoo and Fn-LSav expanded. Nama-Karoo and Fn-LSav probably covered a surface area larger than at present during MIS 5 warm substages, as indicated by up to 70% pollen from this biome during MIS 5 compared to 35% in the core-top samples. This is despite the difference in precession parameters between the last millennium and MIS 5 warm substages. Recent model experiments on the impact of precession changes on southern African vegetation indicate that high precession is linked to reductions of the Bd-LSav (Woillez et al., 2014). Altogether these vegetation changes point to increased aridity in southwestern Africa during the warmest periods of the last interglacial.

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During glacial isotopic stages, contractions of the Nama-Karoo and Fn-LSav would result from a different atmospheric configuration (Fig.5b): a southward migration of the ITCZ and the associated African monsoon (Daniau et al., 2013; Partridge et al., 1997) increasing austral-summer rainfall over southern Africa; an intensification of BUS and decreased SST off the Namibian coast (Stuut and Lamy, 2004; Kirst et al., 1999) leading to aridification of coastal areas; and lastly, an equatorward migration of the westerlies increasing austral-winter precipitation and allowing a

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northward expansion of the winter-rain zone in southern Africa (Chase and Meadows, 2007). The proposed glacial precipitation changes are consistent with recent estimates of Last Glacial Maximum palaeoprecipitation based on glacier reconstruction and mass-balance modelling (Mills et al., 2012), with leaf-wax reconstructions of hydroclimate (Collins et al., 2014), and with simulated glacial climatic fluctuations in southern Africa (Huntley et al., 2014).

The pollen record from MD96-2098 also suggested glacial expansions of Fynbos (Fig.4b), as pollen percentages of *Artemisia*-type, *Stoebe*-type, *Passerina* and Ericaceae were higher during MIS 6, 4 and 3 than in the core-top samples (Fig. S2). These results were consistent with glacial northward expansions of Fynbos documented in other pollen records from southern Africa (Shi et al., 2000; Dupont et al., 2007). Our record also documented a large peak in Fynbos indicators (Fig.4b) that coincided with a fast decrease in Nama-Karoo and fine-leaved savanna pollen percentages at the MIS 5e/5d transition (c. 117 ka), a precession and eccentricity maxima (Laskar, 1990), and an accelerated cooling in Antarctica (EPICA, 2006; Masson-Delmotte et al., 2010) (Fig.4c). As pollen percentages of *Artemisia*-type obtained from surface samples were associated with the Fynbos biome and austral-winter precipitation (Fig. S4 and S5), it cannot be discarded that this peak resulted from a rapid and short-lived expansion of the winter-rain zone of southern Africa. Transitions MIS 6/5 and 4/3 were characterized by small but rapid increases in *Podocarpus*, potentially linked to a short increase in annual precipitation. Such increases in *Podocarpus* have also been documented in other records from southern Africa (Dupont, 2011).

Finally, the amplitude of millennial-scale vegetation changes increased between ca. 100 ka and ca. 25 ka, and was highlighted by switches from negative to positive DCA1 scores (Fig.4b) and increased variability of Restionaceae pollen percentages. Increased Restionaceae pollen could indicate expansions of Fynbos vegetation, or enhanced pollen transport from the Fynbos region linked to increased trade-wind strength (see additional discussion on present-day pollen-vegetation-climate relationships in the Supplementary material). Other Fynbos indicators did not display the same trend (Fig. 4), suggesting that Restionaceae variability between 100 ka and 24 ka were more

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likely the result of enhanced variability of southeast trade winds. Restionaceae pollen percentage data from a record two degrees of latitude north of our marine site also showed comparable increases in the amplitude of millennial-scale changes (Shi et al., 2001). Grain-size wind strength tracers from the Walvis Ridge also displayed enhanced millennial-scale variability, although only after ca. 80 ka (Stuut and Lamy, 2004). An analysis of BUS dynamics over the past 190 ka found increased millennial-scale variability of wind strength after ca. 100 ka and the highest wind strength in this zone during MIS 4 and 3 (Stuut et al., 2002). Such millennial-scale atmospheric reorganisations were probably recorded in the pollen-based DCA analysis as rapid biome shifts in southwestern Africa.

5. Conclusions

Terrestrial and marine markers from the marine core MD96-2098 documented expansions of the Nama-Karoo and fine-leaved savanna during MIS 5e, 5c and 5a warm substages. Northwestern expansions of the Nama-Karoo and Fn-LSav are potentially linked to the reduction of BUS and a local increase in humidity in the desert area, while aridification increased at a regional scale. Towards the east, Nama-Karoo and Fn-LSav expansions probably resulted from increased subtropical high pressure, a northward shift of the ITCZ, and reduced austral-summer precipitation. Nama-Karoo and Fn-LSav expansions to the southern boundary are possibly associated with southern displacement of the westerlies and the subtropical front, decreasing austral-winter precipitation.

During glacial isotopic stages MIS 6, 4 and 3, Fynbos biome expansions are probably linked to the increased influence of the southern westerlies and austral-winter precipitation in southwestern Africa. Our pollen record also suggested that warm-cold or cold-warm transitions between isotopic stages and substages were punctuated by short increases in humidity. Increased variability of vegetation changes at millennial timescales ca. 100 ka was also documented and could be associated with previously-identified enhanced variability of the southeastern trade winds.

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Interglacial-glacial southern Africa biome dynamics were linked to atmospheric and oceanic dynamics resulting from changes in global ice volume and precession at orbital timescales. Atmospheric configurations with westerly winds shifted southwards relative to today have been suggested for other interglacials (Peeters et al., 2004) and are projected for the end of 21st-century under current global warming (Beal et al., 2011). This is likely to reduce austral-winter precipitation over southern Africa and favour expansions of the Nama-Karoo at the expense of the winter-rain fed Fynbos and Succulent-Karoo biomes. However, taking the current orbital configuration alone, the Nama-Karoo and fine-leaved savanna in southern Africa might naturally remain relatively reduced for several millennial ahead.

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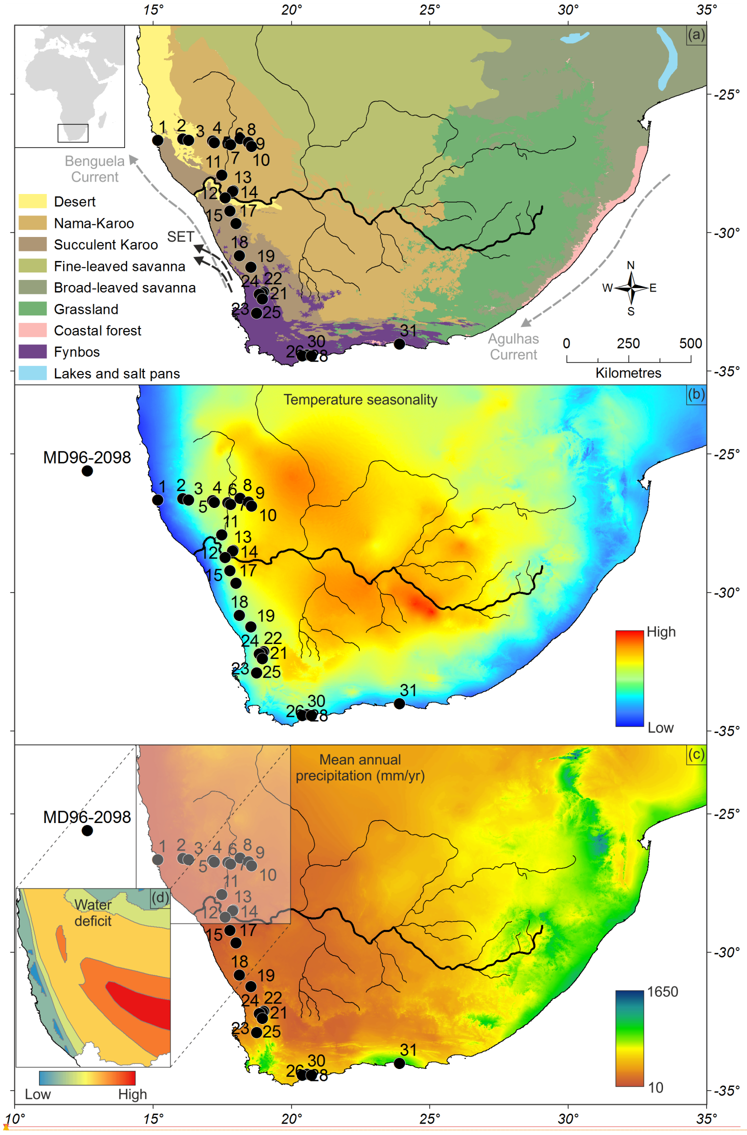

Figure 1. (a) Map of biomes of southern Africa based on Mucina et al. (2007) and modified using the savanna classification by Scholes (1997), location of the Orange River and major tributaries, oceanic currents (grey arrows) and southeastern trade winds (black arrows). Temperature seasonality (b) and annual precipitation in mm yr^{-1} (c) extracted from the WorldClim dataset (Hijmans et al., 2005). Water deficit data (c) redrawn from Barnard (1998) and Digital Atlas of Namibia (http://www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia).

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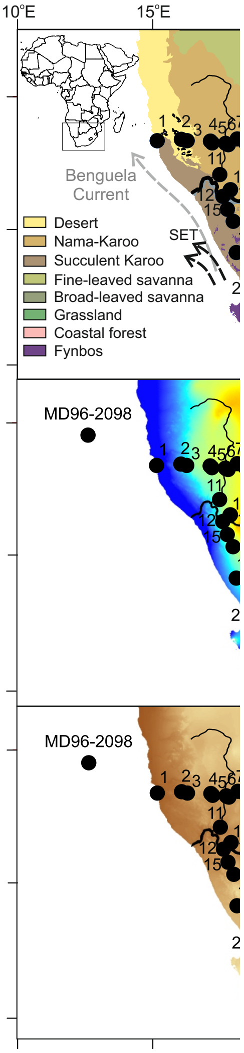

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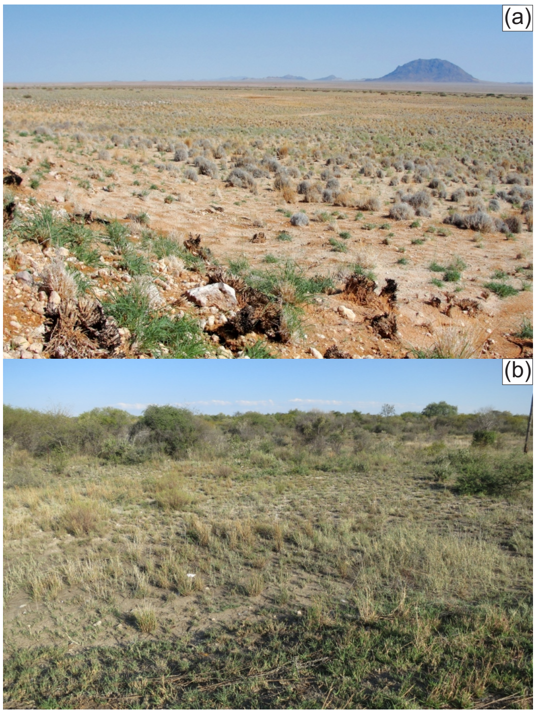

Figure 2. (a) Grass-dominated Nama-Karoo vegetation near Grunau, Namibia. Photo: D.H. Urrego. (b) Grass-dominated fine-leaved savanna vegetation in the Kalahari region of Namibia. Photo: F. D'Errico.

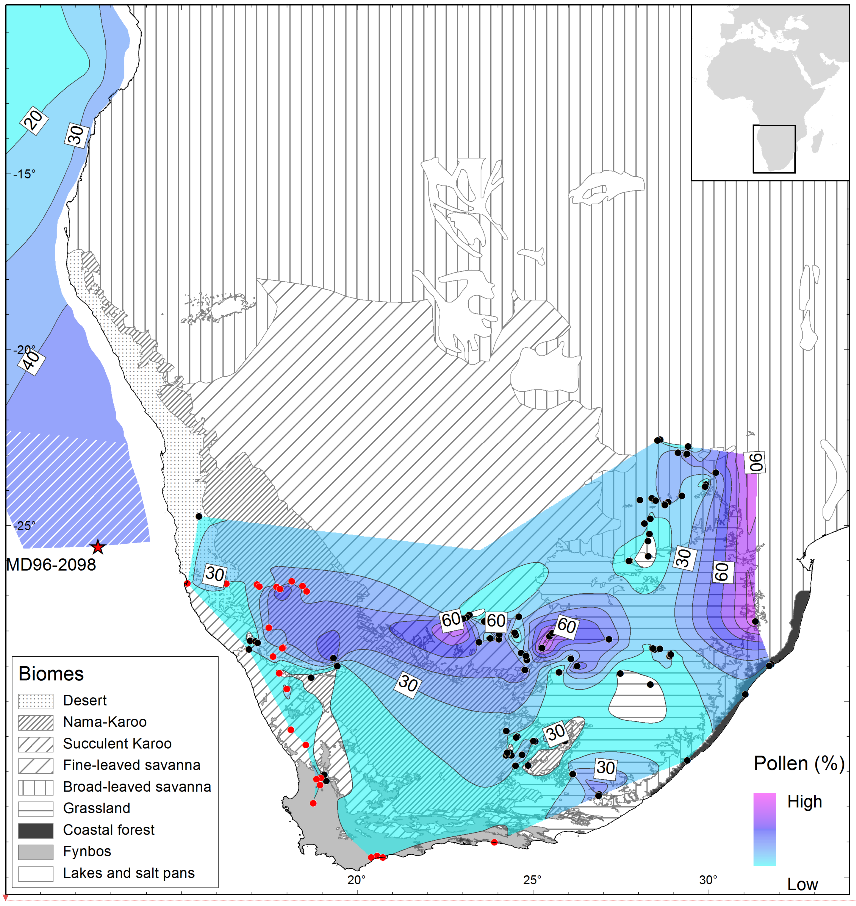

Figure 3. Poaceae pollen percentage iso-lines drawn over biome units of southern Africa (modified from Scholes (1997); Mucina et al., (2007)). The broad-leaved savanna distribution includes the Mopane and mixed savannas described by Scholes (1997). Iso-lines are plotted based on pollen percentage data from surface samples analysed in this study (red dots) and pollen spectra from other samples previously published and extracted from the African Pollen Database (black dots) (Gajewski et al., 2002). Poaceae pollen percentage in the marine domain are redrawn from Dupont and Wyputta (2003) and extended to latitude 25°S using two MD96-2098 core-top samples (hatched).

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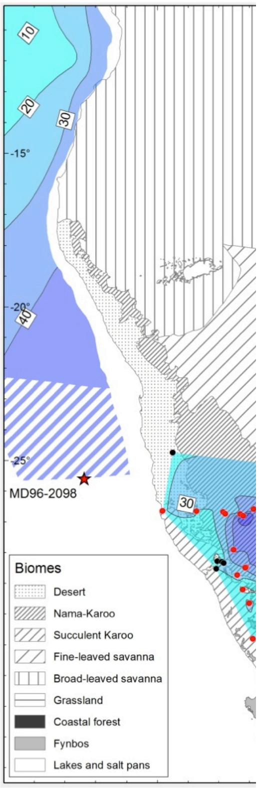

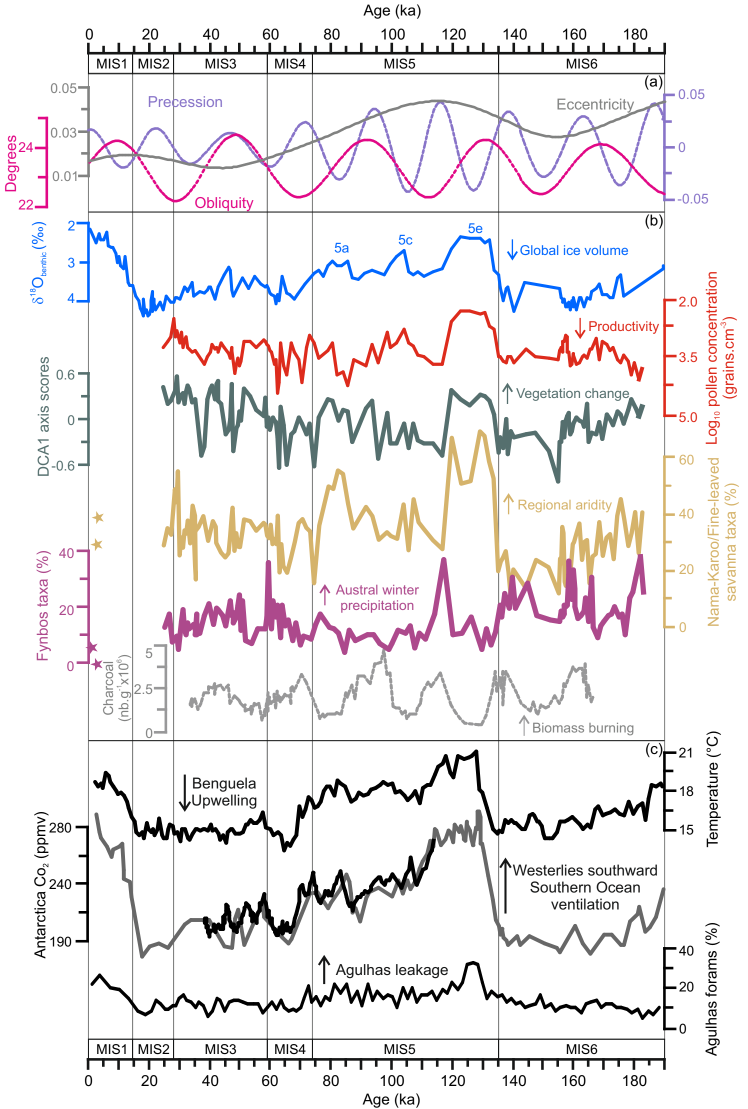

Figure 4. Terrestrial, atmospheric and oceanic markers from southern Africa plotted against age in ka (thousands of calibrated/calendar years before present). (a) Orbital parameters plotted for latitude 25°36'S using La2004 (Laskar et al., 2004). (b) Stable Oxygen profile of benthic foraminifera *Cibicidoides wuellerstorfi* (Bertrand et al., 2002), log-transformed total pollen concentration plotted on an descending scale, detrended correspondence analysis Axis1 scores, pollen percentages of indicator taxa for Nama-Karoo and fine-leaved savanna (Acanthaceae,

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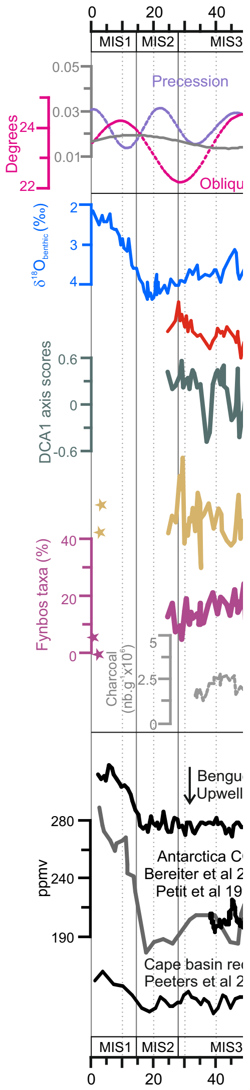

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Aizoaceae, Crassulaceae, Euphoria, Poaceae, and *Tribulus*,) and Fynbos (*Artemisia*-type, Ericaceae, Passerina, *Protea*, and *Stoebe*-type), charcoal concentrations in number of particles per gram (nb.g^{-1}) from marine core MD96-2098 indicating biomass burning (Daniau et al., 2013). Stars on the left correspond to percentage of pollen taxa in two top-core samples dating 530 and 1060 calibrated years before present. (c) Independent climatic records discussed in the text: Alkenone-based SST record from GeoB1711-3 indicating the strength of the Benguela Upwelling system (Kirst et al., 1999), Antarctica CO2 record, gray curve: low-resolution record from Vostok (Petit et al., 1999); black curve: high-resolution EDML-Talos Dome Antarctic Ice Core CO_2 data (Bereiter et al., 2012), and Cape Basin spliced record of planktic foraminifera assemblages indicating the strength of the Agulhas leakage (Peeters et al., 2004). Stage boundary ages for 3/2, 4/3, and 5/4 from (Sanchez Goñi and Harrison, 2010) and 6/5 from (Henderson and Slowey, 2000).

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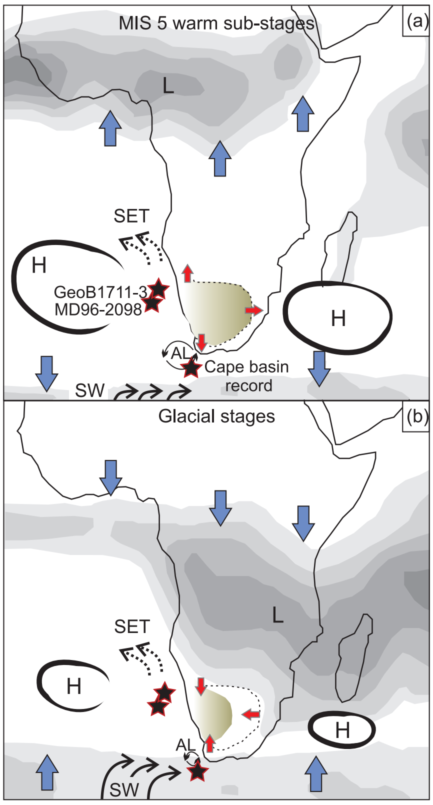

Figure 5. Schematic and simplified configuration of vegetation, atmospheric, and oceanic systems over southern Africa during (a) the MIS 5 warm substages, and (b) glacial isotopic stages. Rainfall is illustrated as grey areas showing the current configuration of tropical and subtropical convection systems using average austral-winter (a) and austral-summer (b) precipitation data between 1979–1995 from the International Research Institute for Climate Prediction (http://iri.ldeo.columbia.edu). L: tropical low-pressure systems, H: subtropical high-pressure systems, SET: southeast trade winds, SW: southern westerlies,

AL: Agulhas leakage. Stars indicate the location of marine records discussed in the text and blue arrows indicate the direction of pressure system migration. Red arrows and brown shaded area indicate hypothesized expansion (a) or contraction of the Nama-Karoo and fine-leaved savanna (b).

Supplementary material

Increased aridity in southwestern Africa during the warmest periods of the last interglacial

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Methods for terrestrial surface-sample collection and analysis

A total of 31 surface samples were collected along a transect from Cape Town (South Africa) to Lüderitz (Namibia) during two weeks of fieldwork in February 2011. The sampling started after the first rains that followed a seven-year long drought. The area extended from latitudes 26.5° to 34.5°S and from longitudes 15° to 23.8°E (Fig.1) and was designed to cover the four major biomes of southwestern Africa (Table S1): Desert, Fynbos, Nama- and Succulent-Karoo. Although we did not conduct a vegetation survey at each sampling site, the surrounding vegetation was determined based on detailed descriptions and maps of southwestern Africa biomes (Mucina et al., 2007). We were also able to collect one sample in the coastal forest biome. While we did not intend to characterize the pollen spectra from coastal forests, including this sample in the dataset allowed increasing the variability of pollen spectra. Sediment and water samples were collected from ephemeral water puddles that developed after rainy episodes and small permanent waterlogged depressions where pollen deposition and preservation was likely. When we found moss attached to rocks or soil, we collected pitches from several spots within a five-meter radius. As a result, our sample set included 12 sediment, 8 moss, and 11 water samples (Table S1).

Surface samples were concentrated down to pellets using a manual and portable centrifuge in the field. Pellets were treated with standard acetolysis in the laboratory (Faegri and Iversen, 1989) and residues were mounted in glycerol and scanned under the microscope at 400 and 1000x magnification. Pollen sums were greater than 300 grains and spores were quantified but excluded from this total. Four out of 31 surface samples had such low pollen concentration that their spectra were excluded from the analysis (Table S1).

We used previously published pollen spectra from 150 additional surface samples collected between 22° and 35° latitude south (APD, Gajewski et al. 2002) to assess the distribution of pollen percentages and potential as indicators of large biomes of seven abundant pollen taxa. These taxa included *Artemisia*-type, Asteraceae-other, Chenopodiaceae-Amaranthaceae, Poaceae, *Podocarpus*, Restionaceae, and *Stoebe*-type. ArcGIS 10 was used to draw iso-lines of pollen percentages by interpolating values from a total of 178 surface samples through the natural neighbour method. Maps of bioclimatic variables were also drawn for comparison.

Table S1. Description of surface samples collected in southwestern Africa and used to characterize the pollen spectra of four southwestern African biomes. Sample number and codes correspond to those of Fig. 1 and 2, and Figures S2 and S3. Samples with low pollen concentration were not assigned a sample code and were not included in the analyses.

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Sample number	Sample code	Latitude	Longitude	Biome	Sample type	Location
1	D1	-26.66	15.17	Desert	Sediment	Luderitz
2	D2	-26.61	16.08	Desert	Water	Namibia semi-desert
3	D3	-26.66	16.28	Desert	Water	Aus savanna
4	Nk4	-26.69	17.15	Nama-Karoo	Water	Buchholzbrunn
5	Nk5	-26.75	17.22	Nama-Karoo	Water	Konkiep
6	Nk6	-26.76	17.71	Nama-Karoo	Sediment	Bethanie
7	Nk7	-26.81	17.81	Nama-Karoo	Water	Seehein
8	Nk8	-26.59	18.14	Nama-Karoo	Sediment	Grunau 2
9	Nk9	-26.73	18.45	Nama-Karoo	Water	Grunau 3
10	Nk10	-26.88	18.57	Nama-Karoo	Sediment	Grunau 4
11	Nk11	-27.92	17.49	Nama-Karoo	Sediment	Fish river canyon
12	Nk12	-28.48	17.90	Nama-Karoo	Sediment	Noodower
13	Nk13	-28.50	17.87	Nama-Karoo	Water	Namibian border
14	Nk14	-28.74	17.61	Nama-Karoo	Sediment	Orange
15	Sk15	-29.21	17.78	Succulent-Karoo	Water	Namaqualand 23
16	-	-29.20	17.78	Succulent-Karoo	Sediment	Swart Doring
0.	Sk17	-29.66	18.00	Succulent-Karoo	Moss	Goegab
18	Sk18	-30.82	18.12	Succulent-Karoo	Sediment	Olifant mouth
19	Sk19	-31.25	18.54	Succulent-Karoo	Moss	Namaqualand
20	-	-31.50	18.31	Succulent-Karoo	Water	Olifant river
21	Fy21	-32.19	18.96	Fynbos	Moss	Cederberg
22	Fy22	-32.23	18.85	Fynbos	Sediment	Typha swamp
23	Fy23	-32.39	18.95	Fynbos	Moss	Citrusdal
24	Fy24	-32.91	18.75	Fynbos	Moss	Piketberg 2
25	Fy25	-32.91	18.75	Fynbos	Moss	Piketberg 1
26	Fy26	-34.41	20.57	Fynbos	Sediment	De Hoop East
27	-	-34.49	20.39	Fynbos	Water	De Hoop reserve
28	Fy28	-34.45	20.40	Fynbos	Moss	De Hoop reserve
29	-	-34.30	20.31	Fynbos	Water	Bree river
30	Fy30	-34.45	20.73	Fynbos	Sediment	Klipdrift river
31	CF31	-34.02	23.90	Coastal forest	Moss	Tsitsikamma-Stormriver

Table S2. Chronological control for marine core MD96-2098 based on unpublished Accelerator Mass Spectrometer radiocarbon dates (AMS^{14}C) and marine isotope events (MIE) identified in the δ^{18}O record from the record of benthic foraminifera *Cibicidoides wuellerstorfi* (Pichevin et al., 2005a; Pichevin et al., 2005b). Calibration details and sources for MIE ages are also shown.

Uncorrected depth (cm)	Corrected depth[1] (cm)	Sample code	AMS^{14}C age/MIE	95.4% (2s) cal age ranges[2]/calendar age (yr BP)	Calibration data[3]/ Source for MIE age
22.5	22.5	SacA 24476	2850±30	2310-2490	Hughen et al. (2004)
65	65	SacA 23251	6105±30	6280-6430	Hughen et al. (2004)
100	100	SacA 26970	8495±40	8750-9020	Hughen et al. (2004)
150	150	SacA 24477	10775±40	11,730-12,080	Hughen et al. (2004)
200	200	SacA 26971	13970±60	16,050-16,860	Hughen et al. (2004)
241	241	SacA 23252	15300±50	17,650-18,070	Hughen et al. (2004)
275	275	SacA 26972	15880±50	18,230-18,290	Hughen et al. (2004)
331	331	SacA 23253	18010±60	20,420-21,220	Hughen et al. (2004)
430.5	430.5	SacA 26973	19150±70	21,850-21,930	Hughen et al. (2004)
481	481	SacA 24478	24200±120	27,990-28,710	Hughen et al. (2004)
561	561	SacA 24479	28890±180	31,910-33,230	Hughen et al. (2004)
601	601	SacA 26974	31870±240	35,130-36,450	Hughen et al. (2004)
647	647	SacA 24480	30430±210*	33,960-34,990	Hughen et al. (2004)
719	704	SacA 23254	40010±520	42,740-44,410	Hughen et al. (2004)
740	725		3.3	46,000	Lisiecki and Raymo (2005)
970	807		3.31	51,000	Lisiecki and Raymo (2005)
1000	837		4	57,000	Lisiecki and Raymo (2005)
1120	957		4.23	64,000	Lisiecki and Raymo (2005)
1195	1032		MIS 5/4	73,500	Sanchez Goñi and Harrison (2010)
1250	1087		5.1	82,000	Lisiecki and Raymo (2005)
1280	1117		5.2	87,000	Lisiecki and Raymo (2005)
1360	1197		5.3	103,800	Drysdale et al. (2007)
1400	1237		5.4	110,400	Drysdale et al. (2007)
1460	1297		Onset of MIS 5	129,000	Masson-Delmotte et al. (2010), Waelbroeck et al. (2008)
1500	1337		MIS 6/5	135,000	Henderson and Slowey (2000)
1560	1397		6.2	140,000	Lisiecki and Raymo (2005)
1600	1437		6.3	155,000	Lisiecki and Raymo (2005)
1730	1567		6.4	160,000	Lisiecki and Raymo (2005)
1800	1637		6.41	166,000	Lisiecki and Raymo (2005)
2020	1857		7.1	192,000	Lisiecki and Raymo (2005)

[1]Corrected depth for gaps reported in stratigraphic log; [2]rounded up to nearest 10 yr; [3]Marine09.14c curve, reservoir age correction = 157 (local delta R) + 400 (Global); *rejected age.

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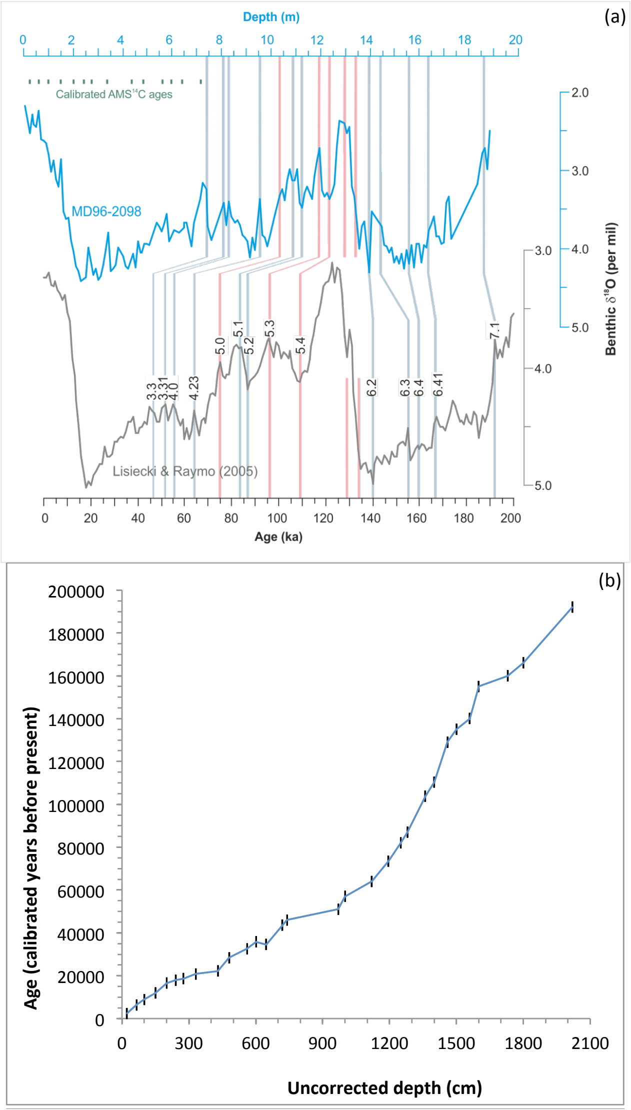

Figure S1. (a) Age control of core MD96-2098 based on 14 calibrated Accelerator Mass Spectrometer radiocarbon (AMS ^{14}C) ages (green dots) and 16 Marine Isotopic Events (MIE, grey and pink bars) from stable Oxygen profile of benthic foraminifera (Bertrand et al., 2002). Radiocarbon ages were calibrated using the Marine09.14c calibration (Hughen et al., 2004; Stuiver and Reimer, 2005), a delta R of 157 years, and global reservoir age of 400 years. Gray bands indicate MIE control points and ages derived from LR04 global stack (Lisiecki and Raymo, 2005). Pink bars indicate MIE ages derived from other chronologies: Sánchez Goñi and Harrison (2010), Drysdale

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et al. (2007), Masson-Delmotte et al. (2010); Waelbroeck et al. (2008), Henderson and Slowey (2000). (b) Age-depth curve including error bars with standard deviation around ^{14}C calibrated ages.

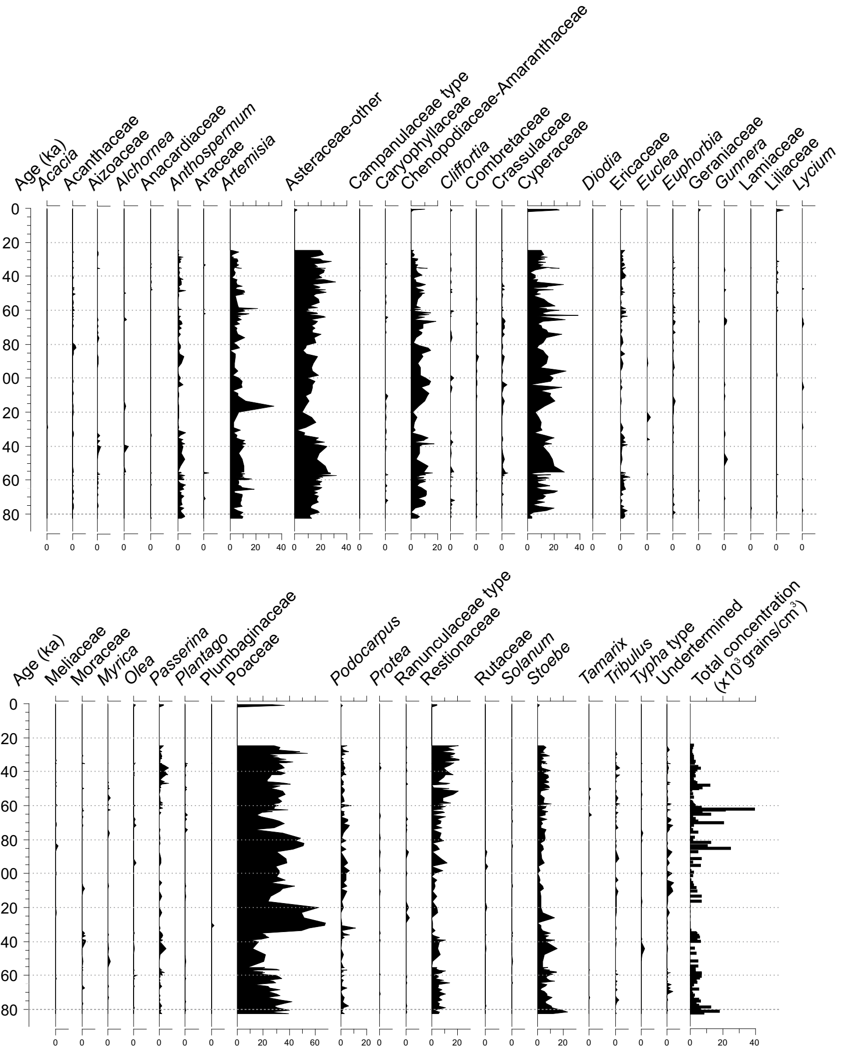


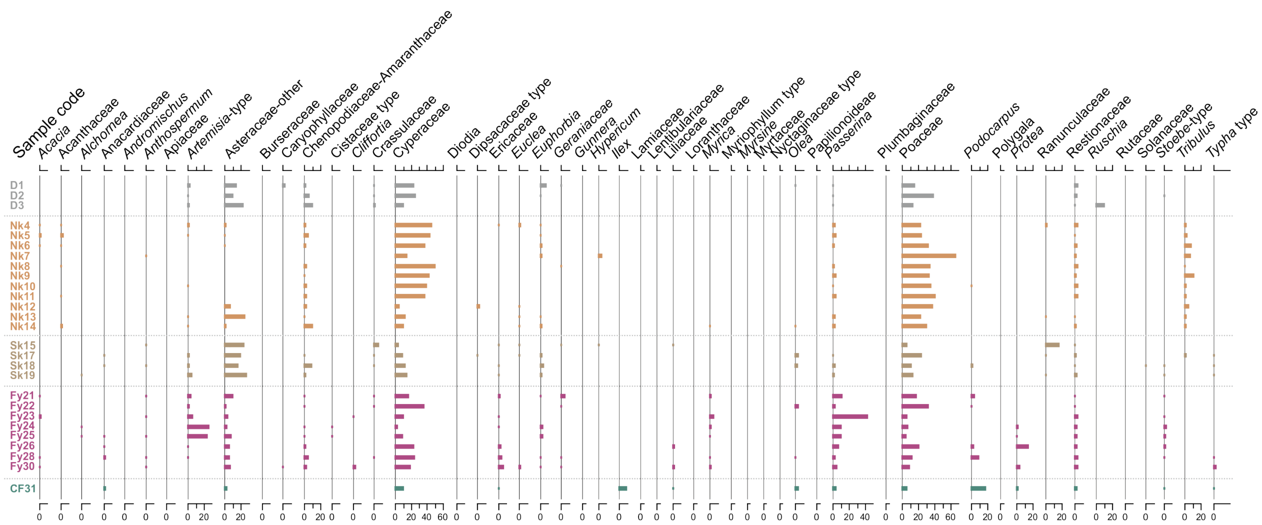
Figure S2. Pollen record and total pollen concentrations from MD96-2098. Percentages from the following families group more than one morphotype: Acanthaceae, Aizoaceae, Anacardiaceae, Asteraceae-other, Chenopodiaceae-Amaranthaceae, Crassulaceae, Cyperaceae, Ericaceae, Liliacaee, and Restionaceae.

Present-day pollen-vegetation-climate relationships in southern Africa

Asteraceae-other, Chenopodiaceae-Amaranthaceae, Poaceae and Restionaceae add up to 80% of the pollen sums and are found in all surface samples (Fig. S3). Cyperaceae pollen is also found in all but one of our surface samples. High Cyperaceae percentages are observed in samples collected from permanent small, waterlogged depressions or along rivers. As a result, we excluded Cyperaceae pollen percentages from ordination analyses.

We decided to include the grasses (Poaceae) in our pollen calibration analysis because they are important components of the southern African vegetation, and not just concentrated around wet areas. Grasses are an incredibly successful group of plants that can be found in many vegetation types around the world, and southern Africa is not an exception. Numerous works on the composition of semi-desert vegetation support this assertion. For instance, Born et al. (2007) reports that the Karoo Region can be distinguished from the other regions by the high proportion of grasses (Poaceae). Cowling and Hilton-Taylor (2009) also describe grasses as being one of the 10 top most abundant families in the Namib-Karoo region. Additionally, Jürgens et al. (1997) reports on the abundance of perennial grasses growing on dunes in the Namibian desert, and Desmet (2007) highlights the dominance of grasses on sandy soils on the Karoo. Our field observations also support this view as we observed large grass-dominated vegetation in the Nama-Karoo areas of southern Africa (Fig.2).

In the surface samples collected in the Desert, Asteraceae-other percentages are up to 20% and Chenopodiaceae-Amaranthaceae percentages are less than 10%. Poaceae and Cyperaceae show up to 45% and between 50 and 60%, respectively. The source of Poaceae, Asteraceae-other and Chenopodiaceae-Amaranthaceae pollen in the Desert can be perennial grasses growing on dunes (Jürgens et al., 1997). Our results show that pollen spectra from the Desert are more similar to spectra from the Succulent-Karoo than to any other biome (Fig. S4), suggesting that Desert surface samples receive pollen from Succulent-Karoo transitional patches.



Supplementary Figure 3. Percentage pollen diagram of taxa ordered alphabetically and identified in surface samples from southwestern Africa. Left column indicates the biome where samples were collected based on Mucina et al. (2007) and sample numbers (see Supplementary Table 1 for sample description); D: desert, Nm: Nama-Karoo, Sk: Succulent Karoo, Fy: Fynbos, CF: coastal forest. Percentages from the following families group more than one morphotype: Acanthaceae, Asteraceae-other, Chenopodiaceae-Amaranthaceae, Crassulaceae, Cyperaceae, Ericaceae, Myrtaceae, Ranunculaceae, Restionaceae, and Solanaceae.

In the Nama-Karoo surface samples, Poaceae pollen reaches percentages up to 60% (Fig. S3). Asteraceae-other pollen percentages are null in northern samples but increase to 20% in samples collected near the Succulent-Karoo. Chenopodiaceae-Amaranthaceae pollen percentages are up to 10%. *Tribulus* and Acanthaceae pollen are only found in the Nama-Karoo samples and reach up to 12%, consistent with their abundance in the vegetation source. On the other hand, Crassulaceae and *Euphorbia* pollen occur at low percentages in samples from Nama-Karoo despite having been described as common in the vegetation (Honig et al., 1992). The pollen spectra from samples collected in the Nama-Karoo form a tight cluster in the DCA ordination and are clearly separated from samples from other biomes (Fig. S4).

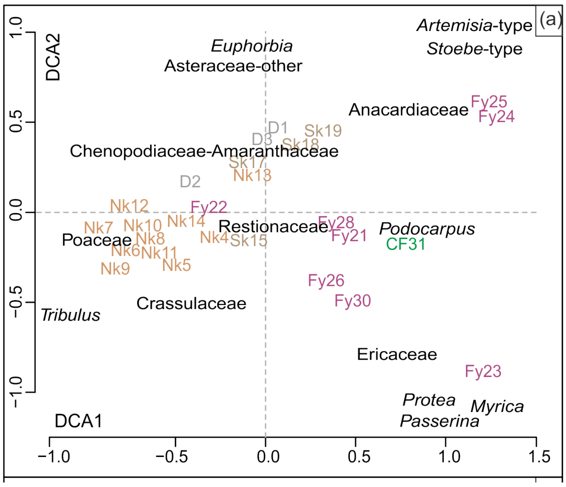


Figure S4. Detrended correspondence analysis summarizing changes in pollen spectra from surface samples collected in southwestern Africa. Sample labels indicate sample numbers and letters indicate biomes where samples were collected: D: Desert, Nk: Nama-Karoo, Sk: Succulent-Karoo Fy: Fynbos, CF: coastal forest. Rescaled species scores are shown for the 15 most abundant pollen taxa.

Surface samples collected in the Succulent-Karoo are characterized by pollen percentages of Asteraceae-other up to 20% and Poaceae between 15 and 20% (Fig. S3). This result corresponds with the abundance of species from the Asteraceae family in this biome, and the relatively less abundance of C4 grasses compared to the Nama-Karoo (Cowling and Hilton-Taylor, 2009). Small percentages of *Olea* and *Podocarpus* also found in the pollen spectra of the Succulent-Karoo could be the result of long-distance wind transport. The DCA ordination groups the Succulent-Karoo pollen spectra near Desert samples, and this clustering is constrained by Asteraceae-other, *Euphorbia* and Chenopodiaceae-Amaranthaceae (Fig. S4).

In surface samples collected within the Fynbos biome, Anacardiaceae, *Anthospermum*, *Artemisia*-type, Ericaceae, *Passerina*, *Protea* and *Stoebe*-type reach highest percentages (Fig. S3). These pollen abundances reflect well the composition of the vegetation source described by (Cowling et al., 1997a), as species of Ericaceae, *Passerina* and *Protea* are particularly characteristic of the Fynbos biome. Up to 10% *Podocarpus* pollen percentages found in the Fynbos likely originate from small forest patches within the area. Poaceae pollen percentages are below 20% in the Fynbos and in the coastal forest sample. *Ilex* pollen is found in the sample from the coastal forest at approximately 5% and *Podocarpus* pollen is up to 18%, consistent with their abundance in the vegetation source. Except for sample Fy22, the composition of pollen spectra from the Fynbos biome in the DCA ordination is clearly distinguished from pollen spectra from other biomes (Fig. S4). The classification of sample Fy22 near samples from the Nama-Karoo likely results from the relatively high abundance of Poaceae pollen in Fy22 compared to other Fynbos samples (Fig. S3).

Some individual taxa are associated with the clustering of pollen spectra from the SWAfr biomes in the DCA ordination (Fig. S4), suggesting their potential as indicators of specific biomes. For instance, Poaceae, Crassulaceae and *Tribulus* obtain the highest loadings to classify the pollen spectra from the Nama-Karoo. Asteraceae-other, Chenopodiaceae-Amaranthaceae and *Euphorbia* are important in the Succulent-Karoo and Desert. Pollen taxa that characterize the Fynbos pollen spectra include Anacardiaceae, *Artemisia*-type, Ericaceae, *Myrica*, *Passerina*, *Protea*, *Stoebe*-type. *Podocarpus* characterizes the pollen spectra from coastal forests and Fynbos biomes.

Pollen percentage iso-lines drawn for six of the most abundant taxa in southern Africa are shown in Fig. S5. These six taxa are also abundant both in terrestrial and marine pollen sequences (Dupont, 2011; Scott et al., 2012) and can therefore be valuable for the interpretation of fossil pollen records. The pollen iso-lines of Asteraceae-other show 25% near the transition of the Nama-Karoo and the Grassland, and 20% in part of the Succulent-Karoo (Fig. S5). Chenopodiaceae-Amaranthaceae pollen percentages are as high as 35% in the Nama-Karoo and are also found up to 50% in a relatively small area of the Desert. This pollen distribution indicates that Chenopodiaceae-Amaranthaceae and Asteraceae-other high pollen percentages can be characteristic of the Succulent-Karoo, Nama-Karoo and Desert biomes of southwestern Africa.

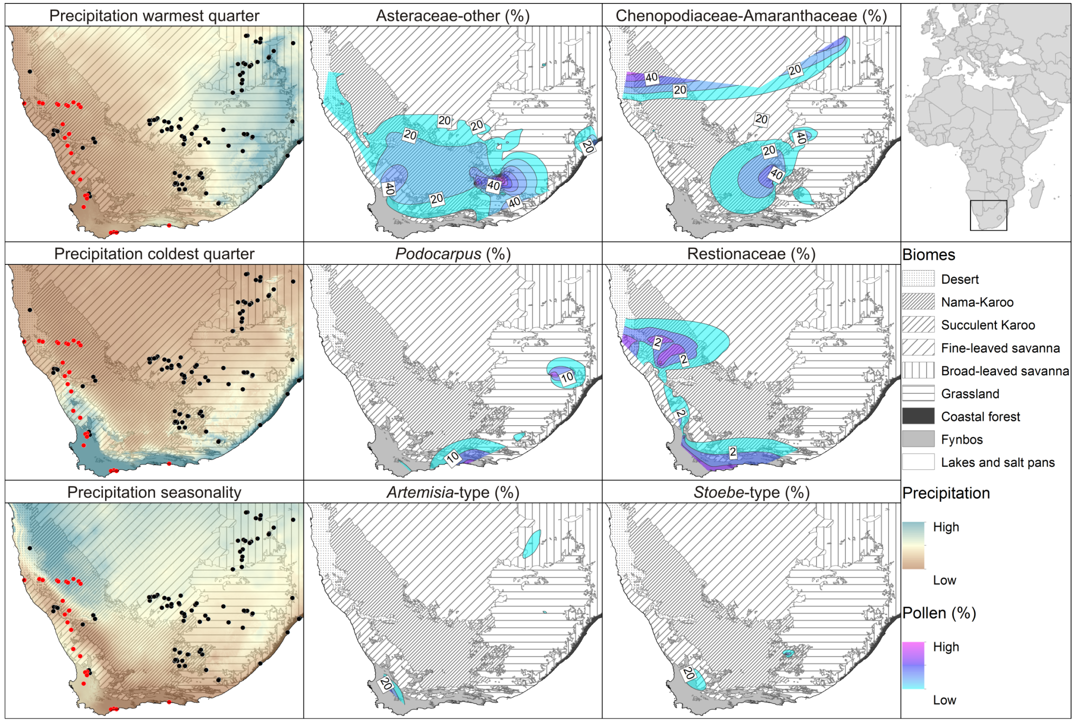


Figure S5. Bioclimatic variables and pollen percentage iso-lines drawn over biome units of southern Africa (modified from Scholes (1997); Mucina et al. (2007)). The broad-leaved savanna distribution includes the Mopane and mixed savannas described by Scholes (1997). Iso-lines are plotted based on pollen percentage data from surface samples analysed in this study (red dots) and pollen spectra from other samples previously published and extracted from the African Pollen Database (black dots) (Gajewski et al., 2002). Numbers and lines represent pollen percentages and are shown for taxa discussed in the text: Asteraceae-other, Chenopodiaceae-Amaranthaceae, *Podocarpus*, Restionaceae, *Artemisia*-type, and *Stoebe*-type.

Podocarpus pollen percentages in surface samples from southern Africa show a localized pattern in areas with high precipitation, namely coastal forest and in the eastern part of the Fynbos biome (Fig. S5). Consistently, (Gajewski et al., 2002) reports maxima of *Podocarpus* pollen percentages in African regions where precipitation is at least 1000 mm per year.

Restionaceae plants are found mostly in the Fynbos biome (Cowling et al., 1997b) and its pollen has been used as a Fynbos indicator (Shi et al., 2001). However, the distribution of its pollen in our surface samples is only partly related to the distribution of the Fynbos biome (less than 5%) (Fig. S5). Up to 5% of Restionaceae pollen is found in surface samples from the Nama-Karoo, Succulent-Karoo and the Desert (Fig. S5). Restionaceae are wind pollinated (Honig et al., 1992), suggesting that these pollen grains are the result of long-distance transport (Fig.1). Due to this inconsistency between the vegetation source and the spatial distribution of Restionaceae pollen, it would be difficult to discern whether increases in Restionaceae pollen in palaeoenvironmental reconstructions are the result of wind strengthening or due to Fynbos vegetation expansions without an independent wind tracer.

The distribution of pollen percentages from *Artemisia*-type and *Stoebe*-type are concentrated in the Fynbos biome (Fig. S5), and are positively correlated with PCQ (Fig. S4). Pollen signals from *Artemisia*-type and *Stoebe*-type, along with other taxa characteristic of the Fynbos vegetation (i.e. Ericaceae, *Protea* and *Passerina*, Fig. S3) might therefore be good tracers for past expansions of the biome.

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