



HAL
open science

Hydroclimate change in subtropical South Africa during the mid-Piacenzian Warm Period

Xueqin Zhao, Andreas Koutsodendris, Thibaut Caley, Lydie Dupont

► To cite this version:

Xueqin Zhao, Andreas Koutsodendris, Thibaut Caley, Lydie Dupont. Hydroclimate change in subtropical South Africa during the mid-Piacenzian Warm Period. *Quaternary Science Reviews*, 2020, 249, pp.106643. 10.1016/j.quascirev.2020.106643 . hal-02989245

HAL Id: hal-02989245

<https://hal.science/hal-02989245>

Submitted on 5 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Hydroclimate change in subtropical South Africa during the**

2 **Mid-Piacenzian Warm Period**

3 Xueqin Zhao¹, Andreas Koutsodendris², Thibaut Caley³, Lydie Dupont¹

4 ¹ MARUM - Center for Marine Environmental Sciences, University of Bremen,
5 Leobener Straße, D-28359 Bremen, Germany

6 ² Institute of Earth Sciences, Heidelberg University, Im Neuenheimer Feld 234-236, D-
7 69120 Heidelberg, Germany

8 ³ EPOC, UMR 5805, CNRS, University of Bordeaux, Pessac, France

9

10 **Abstract**

11 The mid-Piacenzian Warm Period (mPWP, 3.264-3.025 Ma) of the Pliocene epoch has
12 been proposed as an analog for future climate scenarios. Disagreement between the
13 paleoenvironmental reconstruction and model simulations of the climate in subtropical
14 regions for this period suggests that more investigation of the subtropical climate
15 variability of the mPWP is needed. This study presents pollen, microcharcoal and
16 benthic foraminifera oxygen isotope records generated from marine sediment cores of
17 International Ocean Discovery Program (IODP) Exp. 361 Site U1479 from the Cape
18 Basin offshore of South Africa for the period between 3.337 and 2.875 Ma. With an
19 average sample resolution of 3 ka, this record represents the highest-resolution record
20 of mPWP vegetation change from the region. Our results indicate that the vegetation
21 during the mPWP was dominated by fynbos (species-rich heathy vegetation in the
22 Cape Floristic Region) with variable proportions of Ericaceae. Moreover, the
23 development of the Afrotropical forest (tall, multilayered indigenous forests in South

24 Africa) reflects shifts in the amounts of precipitation between winter and summer in the
25 year-round rainfall zone. The vegetation variation is probably influenced by the
26 latitudinal insolation gradient in response to precession forcing. Several glacials
27 depicted by the benthic foraminifera oxygen isotope record were characterized by
28 lower percentage values of Restionaceae, higher percentage values of ericoid fynbos
29 and Afrotropical forest. These events correspond well with cooler SE Atlantic sea
30 surface temperatures driven by interactions of both atmospheric and oceanographic
31 processes. The cooler sea surface temperatures attributed to Antarctic ice sheet
32 expansion, reduced Agulhas leakage (heat and salt transfer from the Indian Ocean to
33 the Atlantic Ocean) and/or intensified southern Benguela upwelling, resulted in less
34 precipitation in the winter rainfall zone of South Africa.

35 Keywords: Vegetation, hydroclimate, mid-Piacenzian Warm Period, IODP Site U1479,
36 South Africa

37 **1. Introduction**

38 The mid-Piacenzian (mid-Pliocene) Warm Period (mPWP, 3.264–3.025 Ma) of the
39 Pliocene epoch was the most recent period in geological history in which global climate
40 was warmer than today as depicted by both paleoclimate data and modelling studies
41 (Haywood et al., 2013). During that period, paleogeography, paleoceanography and
42 paleobiology were the same or very similar to the modern situation (Crowley, 1996)
43 making the mPWP a suitable analog for future climate scenarios (Haywood et al., 2009,
44 2013). On this basis, the mPWP has become the focus of comparative and detailed
45 numerical climate modelling and data/model comparisons. The simulated global
46 temperatures during the mPWP were approximately 2–3°C higher than today
47 (Haywood and Valdes, 2004) and atmospheric CO₂ concentrations (between 330 and
48 400 parts per million) were estimated to be 50-120 ppm higher than pre-industrial levels
49 (275-285 ppm) and probably close to today's level (Pagani et al., 2010). Average global
50 sea level was 10–40 m higher than today (Raymo et al., 2011), the extent of continental
51 ice sheets was limited (Dolan et al., 2011), and the Atlantic meridional overturning
52 circulation (AMOC) was comparable to or stronger than during pre-industrial times
53 (Raymo et al., 1996).

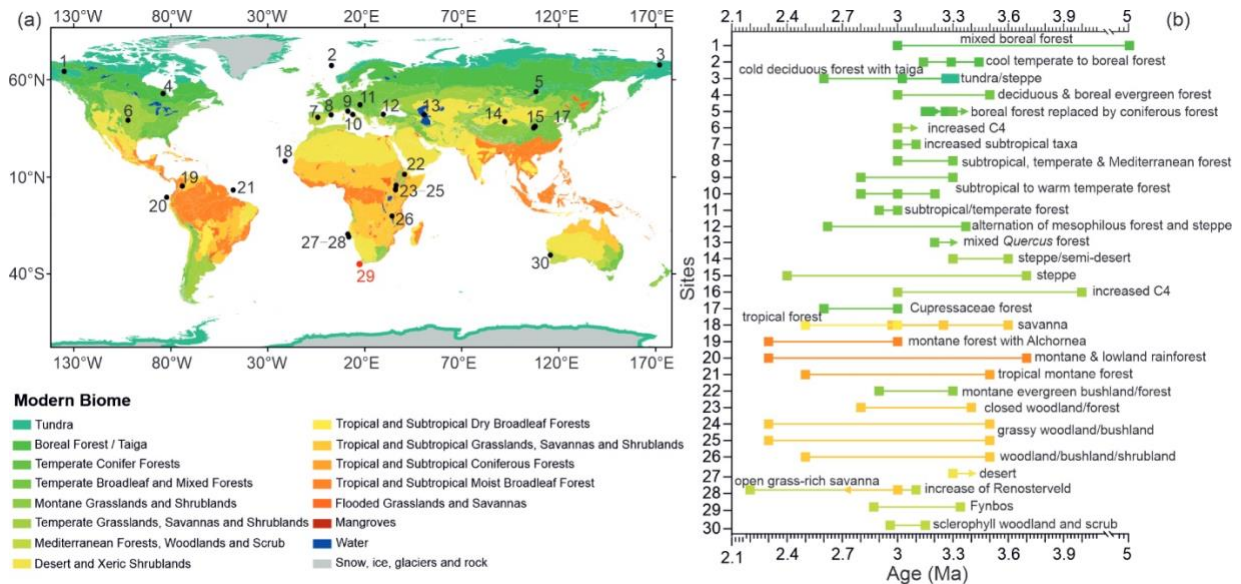
54 However, it remains unclear what mechanisms drove the amplification of warm
55 conditions during the mPWP. Previous studies including paleoclimate modelling,
56 micropaleontological paleotemperature records and paleo-CO₂ estimates based on the
57 boron isotopes of planktic foraminifers, have focused on the role of the atmosphere
58 and oceans, in particular that of ocean-atmospheric CO₂ levels and changes in the
59 meridional ocean heat flux (Bartoli et al., 2011; Dowsett et al., 1992; Rind and Chandler,
60 1991). Later studies, however, suggest additional drivers of the warmer Pliocene
61 conditions independently or in combination with CO₂ concentration variations

62 (Haywood et al., 2009). Salzmann et al. (2008) proposed that the potential causes for
63 the mPWP have only been partially identified. These causes may relate to a
64 combination of changes in orography, atmospheric CO₂ concentrations, water vapor
65 content, ocean circulations and ocean heat transport (Crowley, 1996; Lunt et al., 2012;
66 Raymo et al., 1996), which in turn affect changes in sea-ice cover, surface albedo,
67 cloud cover and temperature (Haywood and Valdes, 2004).

68 Although the climate of the middle Pliocene is relatively stable compared to the
69 Quaternary, it does display climate variability on orbital timescales (Lisiecki and Raymo,
70 2005), which can be interpreted to represent glacial-interglacial periods (Lunt et al.,
71 2012). Just prior to the mPWP, the middle Pliocene was interrupted by a short intense
72 global glaciation (3.305–3.285 Ma) during marine isotope stage M2 (MIS M2) (Lisiecki
73 and Raymo, 2005), which may be seen as a premature step of the climate system in
74 establishing an ice age world (De Schepper et al., 2009; Prell, 1984). The mPWP
75 encompasses six interglacials and glacials including the glacial MIS KM2. Earlier
76 studies compared separately modelled interglacials within the mPWP. The results
77 show that different orbital boundary conditions lead to considerable differences in
78 simulated climate and vegetation between the warm stages (Prescott et al., 2018).

79 We collected summarized paleovegetation studies of the middle and late Pliocene
80 based on pollen or carbon isotopic composition of pedogenic carbonate and mammal
81 teeth. The results show consistency with modern vegetation (Figure 1), however, due
82 to the lack of records in the southern hemisphere, it should be interpreted with caution.
83 Many paleoclimate studies indicate that the vast northern and southern subtropical
84 regions were wetter during the Miocene and Pliocene with a spread of tropical
85 savannahs and woodland where subtropical deserts and arid regions exist today
86 (Salzmann et al., 2008), in particular in Africa (Levin, 2015) and Australia (Martin, 2006).

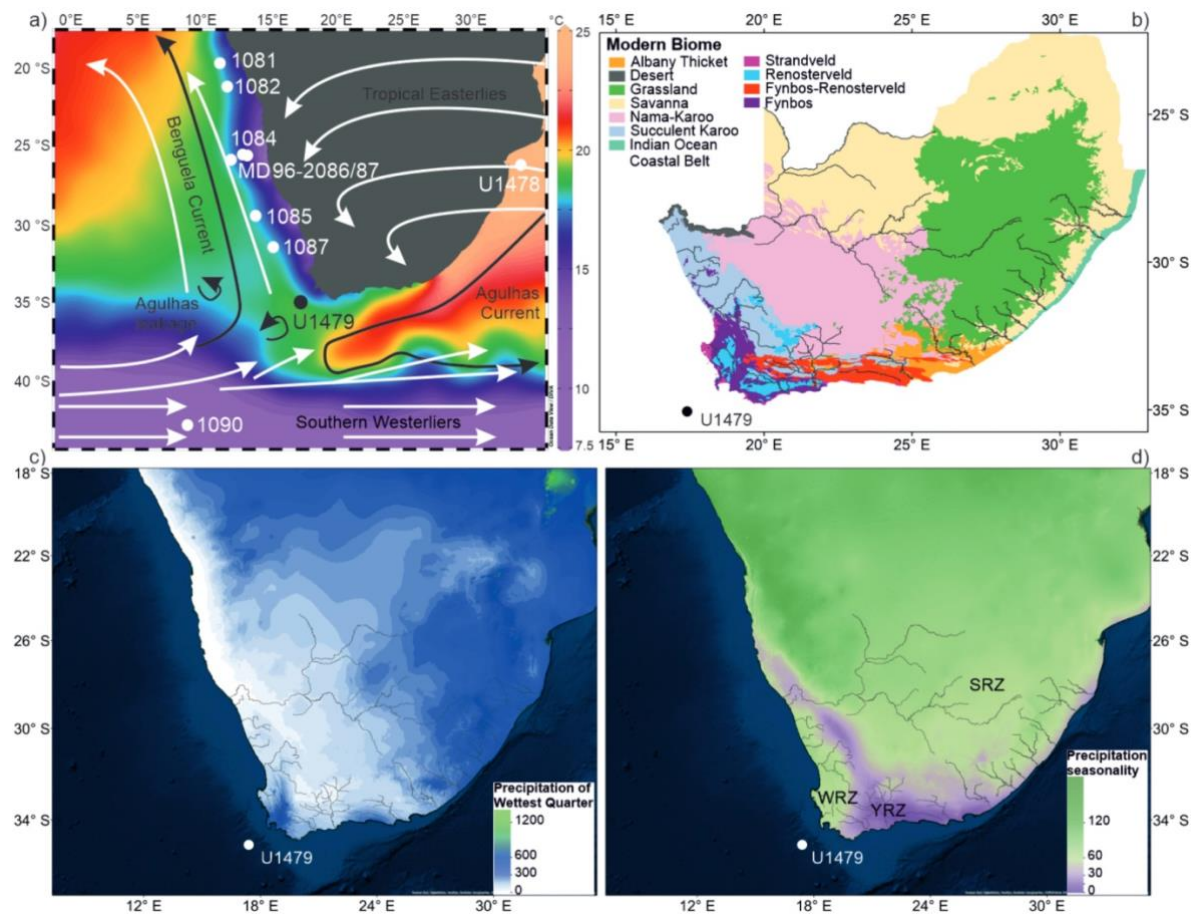
87 However, most models predict drier conditions during past warm climates including the
 88 warm Pliocene (Lau et al., 2013). This puzzle is explained by weaker atmospheric
 89 circulation in response to reduced meridional and zonal temperature gradients (Burls
 90 and Fedorov, 2017).



91
 92 **Figure 1.** Modern biomes (a) and paleovegetation records between 5 and 2.2 Ma (b). The colors in (b)
 93 correspond to the modern terrestrial biomes which are derived from the World Wildlife Fund (WWF)
 94 ecoregions depicted in (a). The Y-axis “Sites” in (b) corresponds to the numbers in (a). Detailed data
 95 sources of (b) can be found in Supplementary file 1.

96 Southern Africa has experienced strong regional differences in moisture availability
 97 (Chase and Meadows, 2007; Zhao et al., 2016b) due to the interactions of both
 98 atmospheric and oceanic circulations between the South Atlantic, Indian and Southern
 99 Oceans. The combination of palynological, geomorphological and sedimentological
 100 evidence indicates warm mesic conditions in southern Africa during the mid-Pliocene
 101 (Scott and Partridge, 1994). A mixture of shrubland (fynbos), woodland and forest
 102 prevailing in South Africa during the mid-Pliocene suggests more humid conditions
 103 (Salzmann et al., 2008). On the other hand, the model study by Prescott et al. (2018)
 104 infers dominance of shrubland and desert instead of forest and woodland in South
 105 Africa during all four mPWP interglacials (G17, K1, KM3 and KM5c). Moreover, other

106 models also predict less annual rainfall and less winter rainfall for Pliocene South Africa
107 (Hunter et al., 2019). First data-model comparisons (the Pliocene Model
108 Intercomparison Project Phase 2; PlioMIP2), mainly concerning sea surface
109 temperatures, have been carried out (Haywood et al., 2020, accepted). The results
110 show significant agreement between simulated and reconstructed temperature change
111 although with notable local signals of data/model disagreement occurring in the
112 Benguela upwelling system. The large data/model discrepancy in the Benguela
113 upwelling system is also observed in SST anomalies focusing on MIS KM5c (3.205 Ma)
114 (the warmest phase of the mPWP), which might be accounted for by a combination of
115 displaced upwelling and warm upwelled water (McClymont et al., 2020). These data-
116 model mismatches indicate that more detailed mPWP hydroclimate reconstructions of
117 subtropical regions are needed, especially in the southern hemisphere where well-
118 dated high-resolution Pliocene paleorecords are scarce. As such, a new record from
119 the South African Cape region at the intersection of the different atmospheric and
120 oceanic systems between the South Atlantic, Indian and Southern Oceans is essential
121 to fill in a gap of information on the southern hemisphere subtropical regions. Thus, to
122 better understand the hydroclimate of subtropical southern Africa during the mPWP,
123 we produced a continuous high-resolution pollen, microcharcoal and benthic
124 foraminifera oxygen isotope record from marine sediment cores of IODP Exp. 361 Site
125 U1479 for the period between 3.337 and 2.875 Ma at millennial-scale resolution (ca. 3
126 ka) (Figure 2). The aim of our study is to assess the variability of vegetation and climate
127 changes in southernmost Africa during the mPWP and to determine possible driving
128 mechanisms.



129

130 **Figure 2.** (a) Map of modern atmospheric and oceanic circulations with modern sea surface
 131 temperatures (World Ocean Atlas 2013) and the location of IODP Site U1479 and the other sites
 132 discussed in this study. (b) Modern vegetation of South Africa with main rivers draining to the ocean
 133 (Mucina and Rutherford, 2006). Modern precipitation of wettest quarter (c) and precipitation seasonality
 134 (d) showing three different rainfall zones in southern Africa derived from WorldClim version 1.3 (Hijmans
 135 et al., 2005). Winter rainfall zone, WRZ, at the southwestern tip of the continent which receives over 66%
 136 of annual rainfall between April and September; year-round rainfall zone, YRZ, which receives both
 137 winter and summer rainfall throughout the year (purple); summer rainfall zone, SRZ, in the rest of the
 138 subcontinent which receives over 66% of annual rainfall between October and March.

139 2. Regional setting

140 2.1 Climate and oceanic circulation

141 Modern climate of southern Africa is controlled by the position and strength of the
 142 South Atlantic and the Indian Ocean anticyclones (Shannon and Nelson, 1996) (Figure

143 2), which results in three different rainfall zones from west to east of South Africa:
144 winter rainfall zone (WRZ), year-round rainfall zone (YRZ) and summer rainfall zone
145 (SRZ) (Tyson and Preston-Whyte, 2000). The pressure difference between the South
146 Atlantic anticyclone and the continental pressure field causes alongshore southeast
147 trade winds (SE trade winds). The SE trade winds drive an offshore, surface-drift
148 inducing Benguela upwelling causing aridity in western southern Africa north of the
149 Cape region. In the Cape region, moisture is mainly supplied by the southern westerlies
150 during austral winter. The northern part of the WRZ is relatively arid due to the all-year
151 influence of the cold waters of the Benguela upwelling system. The influence of
152 westward to south-westward directed offshore winds (known as Berg winds) is very
153 limited because they are blocked by the southern westerlies and almost no dust plumes
154 can be observed south of 28°S (Eckardt and Kuring, 2005). The SRZ receives most of
155 its rainfall from tropical moisture easterlies during austral summer. In contrast to the
156 pronounced seasonality in the WRZ and SRZ, an intermediary area between them is
157 the YRZ influenced by the interaction of both temperate and tropical circulation
158 systems. In the YRZ, at least 11 but mostly all 12 months of the year contribute 5% or
159 more to the long-term average of the total annual rainfall during 1979–2011
160 (Engelbrecht et al., 2015).

161 Rainfall amounts, seasonality and distribution patterns in southern Africa are further
162 influenced by two major oceanic circulation systems (Figure 2). One is the northward
163 flowing Benguela Current (BC) along the west coast of southern Africa, the other is the
164 Agulhas Current (AgC) (Nelson and Hutchings, 1983; Shannon and Nelson, 1996). At
165 the southern boundary of the Benguela upwelling system, the relatively cool and
166 oligotrophic waters of the South Atlantic Current and the cold waters of the Antarctic
167 Circumpolar Current meet the south-westward flowing warm and saline waters of the
168 Agulhas Current. Most of the AgC waters are retroflected to the south and east forming

169 the Agulhas Return Current, while a small part of the AgC continues in a north-westerly
170 direction through the South Atlantic Ocean in the form of eddies. The leakage is
171 determined mainly by the latitudinal position and intensities of the southern westerlies.
172 During austral summer, the southward contraction and intensification of the southern
173 westerlies would favor more Agulhas leakage, coinciding with aridity in the WRZ
174 (Biaستoch et al., 2009; Durgadoo et al., 2013).

175 IODP Exp. 361 Site U1479 is located on the western slope of the Agulhas Bank in
176 Cape Town under the pathway of mixed water masses: southward flowing North
177 Atlantic deep water, cold northward-flowing Benguela Current, warm and salty Agulhas
178 leakage (Hall et al., 2017).

179 **2.2 Vegetation and fire**

180 The strong west-east gradient in rainfall amount and seasonality has a great effect on
181 the vegetation resulting in nine biomes in southern Africa (Figure 2) (Cowling et al.,
182 1997; Mucina and Rutherford, 2006). The continental area near the study site is
183 dominated by vegetation types including Fynbos, Renosterveld, Succulent Karoo and
184 Nama Karoo. In addition, small patches of Afrotropical Forest occur.

185 Subtropical regions are equatorward defined by the transition from subtropical to
186 tropical (monsoonal) climates. The rainfall season changes from summer rains in the
187 tropics to winter rains in the subtropics, which has a large impact on vegetation. In
188 southern Africa, the subtropical winter rainfall zone (Chase and Meadows, 2007) is
189 nowadays restricted to the Western and Southern Cape Province, which is mainly
190 dominated by fynbos (Linder, 2003). **Fynbos** is a species-rich heathy vegetation,
191 which was established in South Africa during the late Miocene (Dupont et al., 2011).
192 The Fynbos biome, part of the Cape Floristic Region, has extremely high levels of
193 species richness and endemism. It is an evergreen, fire-prone shrubland in the

194 southwest Cape, which is typified by the presence of restios (wiry, evergreen
195 graminoids of the Restionaceae), a high cover of ericoid shrubs (fine-leaved shrubs of
196 Ericaceae, Asteraceae, Rhamnaceae, Thymelaeaceae and Rutaceae), and the
197 common occurrence of proteoid shrubs (Proteaceae). Rainfall usually varies from 600
198 to 800 mm/yr. Other important features of fynbos are the presence of leaf spinescence,
199 high sedge (Cyperaceae) cover and low grass (Poaceae) cover (Mucina and
200 Rutherford, 2006). Fynbos is found especially along the southwestern and southern
201 coast of South Africa and thus receives most rainfall during austral winter.
202 **Renosterveld** is an evergreen, fire-prone shrubland or grassland, which is dominated
203 by small, cupressoid-leaved and evergreen asteraceous shrubs (principally
204 renosterbos, *Elytropappus rhinocerotis*). Other important shrub represented in
205 renosterveld include Boraginaceae, Fabaceae, Malvaceae, *Cliffortia* and
206 *Anthospermum* (Goldblatt and Manning, 2002). The **Succulent Karoo** biome, located
207 in a narrow strip inland of the west coast, is a semidesert region characterized by dwarf
208 leaf-succulents of which Aizoaceae (including Mesembryanthemoideae) and
209 Crassulaceae are particularly prominent; many other families are also common
210 including Asteraceae, Amaranthaceae, Euphorbiaceae (*Euphorbia*) and
211 Zygophyllaceae (*Zygophyllum*) (Wheeler, 2010) but grass cover is low. In comparison
212 to the Fynbos biome, the Succulent Karoo biome is better adapted to arid conditions
213 and higher summer temperatures (Carr et al., 2014), receiving most of the rainfall
214 during austral winter. The **Nama Karoo** biome, which is a semi-desert dwarf and
215 grassy shrubland found on the central plateau, is dominated by Asteraceae, Poaceae,
216 Aizoaceae, Liliaceae and Scrophulariaceae. The Nama Karoo biome located northeast
217 of the study area, receives rainfall mainly during austral summer. The **Afrotemperate**
218 **Forest** biome, which is restricted to areas with mean annual rainfall of more than 725
219 mm in the SRZ and more than 525 mm in the WRZ (Mucina and Rutherford, 2006)

220 comprises mostly of evergreen trees in multi-layered canopies, while the ground layer
221 is often poorly developed due to the dense shade. The southern Afrotemperate forest
222 occurs in patches near Port Elizabeth in the east to Cape Peninsula in the west along
223 the feet of south and east-facing slopes, and in ravines and deep gorges of the Cape
224 Fold Belt mountains (Bergh et al., 2014). These forests reach their greatest extent in
225 the southern Cape along the narrow (ca. 250 km long) coastal strip between
226 Humansdorp in the east to the west of Mossel Bay (Bergh et al., 2014).

227 Fire is important in the fynbos ecosystem, which burns on a 5–50 year rotation, usually
228 in the order of 15–25 years (Mucina and Rutherford, 2006). Fire regimes in
229 Renosterveld are largely unknown; it is however assumed that fire rotation lies within
230 a 2–10 year range. Presently, fires occur in late summer and early autumn, towards
231 the end of the dry season naturally due to sparks of rockfalls and lightning (Bond, 1996;
232 Van As et al., 2012).

233 The YRZ also plays an important role in fostering the extraordinary botanical diversity
234 of the region (Mucina and Rutherford, 2006; Bergh et al., 2014). In the southern Cape
235 region, there is a mosaic of various vegetation types of fynbos as well as Afrotemperate
236 forest and coastal thicket. Generally, Afrotemperate forest patches require the highest
237 values of soil moisture (average annual rainfall varies between 500 and 1200 mm)
238 (Mucina and Rutherford, 2006) and are thus most prominent in the valleys, whereas
239 fynbos and coastal thicket occur in the coastal lowlands and dunes (Quick et al., 2018).
240 Afrotemperate forest in this region can be found within the Touws River and Duiwe
241 River valleys which are dominated by *Afrocarpus falcatus*, *Podocarpus latifolius* and
242 *Olea capensis* (Cowling et al., 1997).

243 **3. Materials and methods**

244 **3.1 Materials and age model**

245 The samples investigated in this study were collected from sediment cores of IODP
246 Exp. 361 Site U1479 (35°03.52'S, 17°24.03'E, ~2630 m water depth). Site U1479 is
247 located in the Cape Basin on a 30 km wide morphological high, rising ~200 m above
248 the regional seafloor on the mid to lower western slope of the Agulhas Bank, ~130 km
249 southwest of Table Mountain and Cape Town, South Africa (Hall et al., 2017). Material
250 from the undisturbed Holes U1479B and U1479C were selected to obtain a complete
251 spliced stratigraphic section from the best core parts using color and natural gamma
252 ray data. The photos of the cores can be found on the IODP website with the following
253 link (http://publications.iodp.org/proceedings/361/EXP_REPT/CORES/IMAGES/). The
254 original meter composite depth was updated to an adjusted, so-called composite depth
255 below seafloor (m CCSF-A). The study interval was first defined based on the
256 shipboard age model, which was developed using bio- and magnetostratigraphy (Hall
257 et al., 2017). The final age model across the study interval was further refined by tuning
258 of benthic foraminifera oxygen isotope curves to the global LR04 benthic $\delta^{18}\text{O}$ stack
259 (Lisiecki and Raymo, 2005) using the AnalySeries software (Paillard et al., 1996) and
260 yielded a correlation coefficient of $R = 0.81$ for the studied time interval. It provides a
261 continuous record between 3.337 and 2.875 Ma. The sedimentation rates of the
262 investigated interval between 141.24 and 164.07 m CCSF-A lie between 4.1 and 6.8
263 cm/ka (an average of 5.0 cm/ka).

264 **3.2 Benthic foraminifera $\delta^{18}\text{O}$ analysis**

265 Specimens of benthic *Cibicides wuellerstorfi* foraminifera were picked from the 250–
266 315 μm size fraction.

267 76 samples were measured with a MultiPrep system on line with a dual Inlet
268 IsoPrime™ Isotope Ratio Mass Spectrometer (IRMS) at the Laboratoire de Geologie
269 of the University of Lyon. Calcium carbonates were reacted with anhydrous phosphoric

270 acid at 90°C to generate CO₂. Isotope compositions are quoted in the delta notation
271 in ‰ relative to Vienna Pee Dee Belemnite (VPDB). Isotopic data result from a one-
272 point calibration using the internal reference 'Carrara Marble' (Analytical standard
273 deviation of 0.05‰ for δ¹⁸O with a carbonate weight >100µg and 0.1‰ with a
274 carbonate weight <100µg), itself regularly calibrated against the international reference
275 NBS19.

276 17 samples were carried out on a Thermo Scientific 253 Plus isotope ratio mass
277 spectrometer coupled to a Kiel IV carbonate device at EPOC laboratory, University of
278 Bordeaux. The automated preparation system (Kiel IV) transforms solid carbonate
279 samples into CO₂ gas by treatment with orthophosphoric acid at a constant
280 temperature of 70°C. The sample CO₂ gas is then transferred using a microvolume,
281 and introduced by dual inlet in the Mass spectrometer to measure its ¹⁸O/¹⁶O isotopic
282 ratio in comparison with a calibrated reference gas. Aliquots of NBS19 standard, which
283 is calibrated against the VPDB, were analyzed with the samples to correct any
284 deviation of the reference gas. Oxygen isotopic ratio values are expressed using the δ
285 notation with a per mil deviation (‰) from VPDB. Analytical standard deviation is ≈
286 0.06‰ for δ¹⁸O.

287 In three of the samples analyzed in this study no *Cibicides wuellerstorfi* could be found.
288 We, therefore, analyzed δ¹⁸O on *Uvigerina peregrina* taxa in the same size fraction.
289 Because *Uvigerina peregrina* is isotopically heavier than *Cibicides* by 0.47‰, we
290 adjusted *Uvigerina peregrina* δ¹⁸O to the *Cibicides* scale by subtracting 0.47‰
291 according to Marchitto et al. (2014). Benthic foraminifera δ¹⁸O are available and stored
292 in the Pangaea database (<https://doi.pangaea.de/10.1594/PANGAEA.919576>).

293 **3.3 Palynological analysis**

294 A total of 151 samples were taken at 15 cm intervals between 141.24 and 164.07 m
295 CCSF-A for palynological analysis, aiming at a temporal resolution of ca. 3 ka. The
296 samples were prepared with the following steps: 1) determination of the sample volume
297 by water replacement; 2) decalcification with diluted cold HCl (~10%) and addition of
298 *Lycopodium* spore tablets (12 samples with 2 tablets of batch Nr. 4832162 and the
299 other 139 samples with 2 tablets of batch Nr. 177745); 3) after washing, the samples
300 were treated with cold HF (~40%); 4) the samples were shaken for 2 hours, and then
301 kept standing for two days to remove silicates; 5) concentrated HCl (~37%) was added
302 to keep fluor-complexes in solution; 6) all samples were first sieved over a 125 µm
303 metal mesh and then sieved over a 7-µm nylon mesh screen while ultrasonically
304 disaggregating organic matter; 7) samples were stored in water, mounted in glycerol
305 and examined under a light microscope (magnification 400 x and 1000 x) for pollen,
306 spores, fresh-water algae, and microcharcoal. Pollen grains were identified using the
307 African pollen reference collection of the Department of Palynology and Climate
308 Dynamics of the University of Göttingen, the African Pollen Database
309 (<http://apd.sedoo.fr/pollen/interface/indexPollen.html>) and literature (Bonnefille and
310 Riollet, 1980; Scott, 1982). Pollen zonation was conducted by Constrained Incremental
311 Sum of Squares Cluster Analysis (CONISS, TILIA 2.0.41, with dendrogram scale of
312 total sum of squares) including all counted pollen and spore taxa (Figure 3). All pollen
313 and spore taxa were included in the pollen sum (ranging between 145 and 347 with an
314 average of 290 per sample) used to calculate pollen percentages. Pollen concentration
315 was determined based on the *Lycopodium* spore counts. Samples volumes were
316 measured using water displacement to calculate concentration values. Pollen
317 accumulation rates were calculated by multiplying the pollen concentration (grains/cm³)
318 by the sedimentation rate (cm/ka) for each sample. The 95% confidence intervals of
319 percentages were calculated following Maher (1972). All counts of pollen and spores

320 are available and stored in the Pangaea database
321 (<https://doi.pangaea.de/10.1594/PANGAEA.919633>). Microcharcoal analysis was
322 conducted on the same slides as the pollen analysis using the 202-touch point count
323 method (Clark, 1982) to calculate the microcharcoal concentration in square
324 centimeter/cubic centimeter (cm^2/cm^3). At least 225 fields per sample were analyzed
325 to improve the statistical reliability of the results. Microcharcoal concentrations are
326 available and stored in the Pangaea database
327 (<https://doi.pangaea.de/10.1594/PANGAEA.919575>).

328 **3.4 Spectral analysis**

329 To analyze cyclicity in the palynological records, we carried out a spectral analysis
330 (window: hanning; oversample: 2; segments: 3) using the module REDFIT (Schulz and
331 Mudelsee, 2002) of the paleontological statistics package PAST vs 3.0 (Hammer et al.,
332 2001).

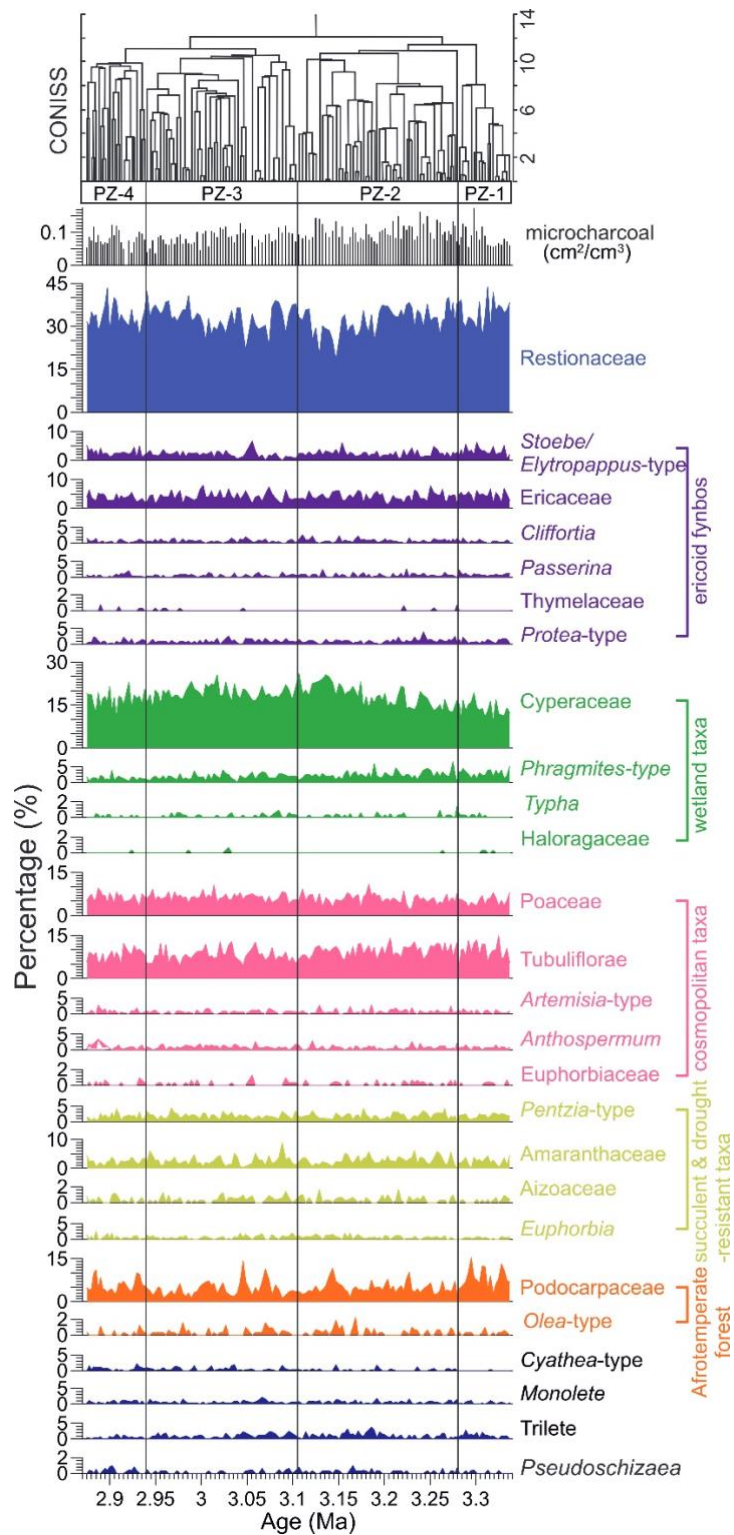
333 A cross spectral analysis between pollen groups and southern hemisphere latitudinal
334 winter insolation gradient (LIG) was also carried out with AnalySeries software (Paillard
335 et al., 1996). Linear interpolation was used to resample data and LIG according to the
336 pollen resolution. For each analysis, B-Tukey spectrum was used within a Bartlett
337 window. The time step used for the B-Tukey analysis is 2000 years. The bandwidth is
338 1.07×10^{-5} , non-zero coherence significant at the 95% confidence level is higher than
339 0.55.

340 **4. Results**

341 Pollen and spores are relatively abundant and generally well preserved in IODP Site
342 U1479 for the period 3.337 to 2.875 Ma. Pollen concentrations range from 289 to 1037
343 grains/ cm^3 with an average of 533 grains/ cm^3 and pollen accumulation rates range

344 from 1.2×10^3 to 5×10^3 grains/cm²/ka with an average of 2.7×10^3 grains/cm²/ka. The
345 pollen diagram of selected pollen taxa for the period from 3.337 to 2.875 Ma is provided
346 in Figure 3. The most abundant pollen taxa throughout the record are Restionaceae
347 (~18–44%, average 33%), Cyperaceae (~9–26%, average 18%), Tubuliflorae (~4–
348 15%, average 9%), Podocarpaceae (~1–15%, average 5%), Poaceae (~2–11%,
349 average 6%). Other common pollen taxa include *Stoebe-Elytropappus*-type (~0–7%,
350 average 2%), Ericaceae (~1–8%, average 4%), CCA (including Amaranthaceae, and
351 Caryophyllaceae) (~0–9%, average 3%), *Cliffortia*-type (~0–3%, average 0.7%),
352 *Passerina* (~0–3%, average 0.6%), *Protea*-type (~0–4%, average 1%), *Phragmitis*-
353 type (~0–7%, average 2%), *Artemisia*-type (~0–3%, average 0.7%), *Anthospermum*
354 (~0–4%, average 0.8%), *Pentzia*-type (~0–4%, average 2%) and *Euphorbia* (~0–3%,
355 average 0.6%).

356 The identified pollen was grouped into vegetation categories (Figure 4) as ericoid
357 fynbos (including *Stoebe-Elytropappus*-type, Ericaceae, *Cliffortia*, *Passerina*, other
358 Thymelaeaceae, *Protea*-type), wetland taxa (including Cyperaceae, *Phragmites*-type,
359 *Typha*, Haloragaceae), cosmopolitan taxa (including Poaceae, Asteraceae
360 Tubuliflorae, *Artemisia*-type, *Anthospermum*, Euphorbiaceae pp), succulent and
361 drought-resistant taxa (including *Pentzia*-type, Amaranthaceae, Aizoaceae, *Euphorbia*)
362 and Afrotropical forest (including Podocarpaceae, *Olea*-type). This grouping is
363 based on the modern pollen distribution in the Namaqualand mudbelt along the west
364 coast of South Africa (Zhao et al., 2016a, 2016b) and on palynological studies from the
365 Cederberg Mountains (Valsecchi et al., 2013) and the south coast (Quick et al., 2018).



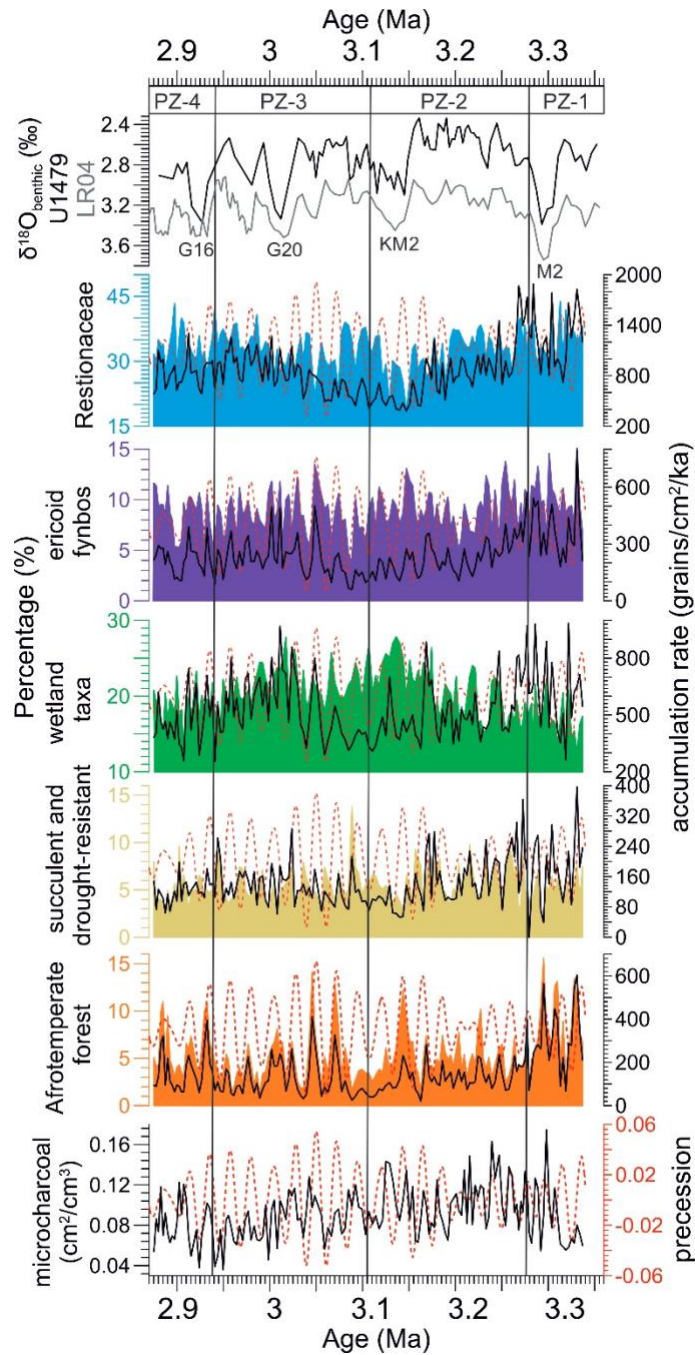
366

367 **Figure 3.** Pollen percentages of selected taxa from IODP Site U1479. Pollen assemblage zones were
 368 derived by CONISS (Grimm, 2015).

369 The record has been divided into four pollen assemblage zones (PZ) using the
 370 CONISS calculation (Grimm, 2015). Zone PZ-1 (3.337–3.280 Ma) is characterized by
 371 pollen percentage maxima of Restionaceae, ericoid fynbos and Afrotropical forest.

372 The percentages of succulent and drought taxa, and Cyperaceae reach minima in this
373 zone. Zone PZ-2 (3.280–3.107 Ma) is characterized by a pollen percentage decrease
374 of Restionaceae reaching minima around 3.147 Ma, while ericoid fynbos reaches high
375 values around the same time. Afrotemperate forest representation has much lower
376 values in PZ-2 than in PZ-1 but shows several peaks. Succulent and drought taxa start
377 to increase to high values between 3.279 and 3.156 Ma. This zone is also
378 characterized by the increase of wetland taxa reaching maxima around 3.136 Ma. In
379 zone PZ-3 (3.107–2.941 Ma), the pollen percentage of Restionaceae starts to increase
380 again, while the percentage of wetland taxa fluctuates around relatively high values
381 with slightly decreasing trend. Succulent and drought taxa fluctuate with no clear trend.
382 Zone PZ-4 (2.941–2.875 Ma) shows alternating percentage maxima of Restionaceae
383 and Afrotemperate forest.

384 Microcharcoal concentration values fluctuate between 0.04 and 0.17 cm²/cm³ with an
385 average of 0.09 cm²/cm³ (Figure 4). Microcharcoal concentrations are characterized
386 by relatively low values at the beginning of the record with a generally increasing trend
387 until 3.239 Ma and a maximum of 0.17 cm²/cm³ at 3.298 Ma. After 3.239 Ma,
388 microcharcoal concentrations start to decline reaching minimum values (0.04 cm²/cm³)
389 at 2.950 Ma which then increase to higher values again after 2.941 Ma.

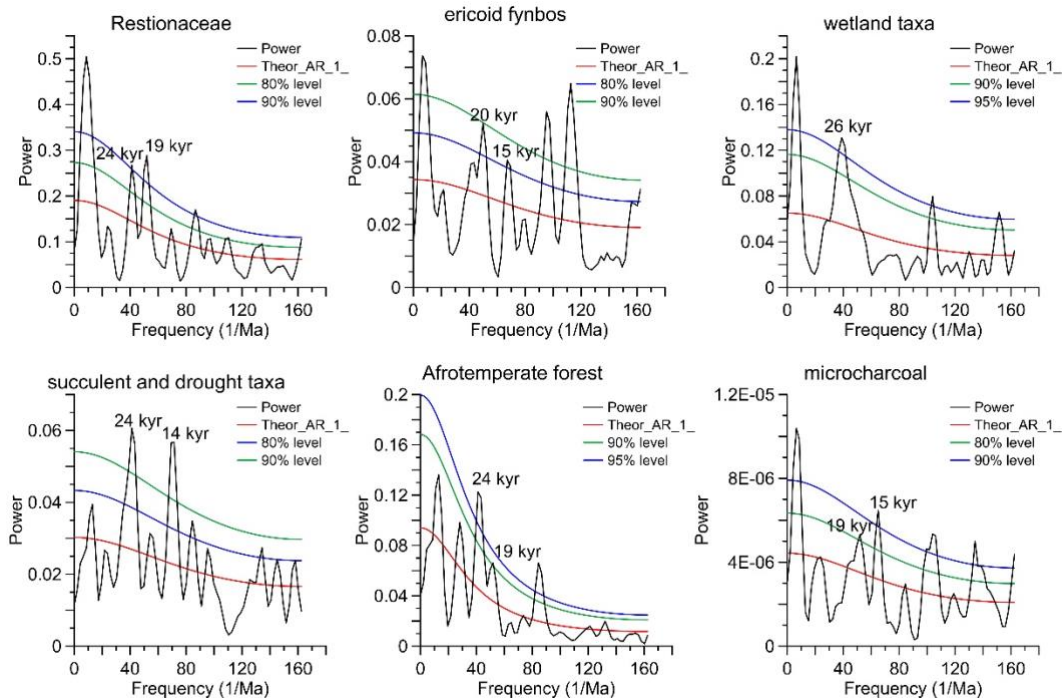


390

391 **Figure 4.** Oxygen isotopes of benthic foraminifera of IODP Site U1479 (black) compared to the global
 392 stack LR04 (gray) (Lisiecki and Raymo, 2005), pollen percentages (shading) and accumulation rates
 393 (lines) of four groups (Restionaceae, ericoid fynbos, wetland taxa and Afrotemperate forest) as well as
 394 the microcharcoal concentrations from IODP Site U1479 overlaid with precession (dashed lines) (Laskar
 395 et al., 2004).

396 The spectral analysis of the Restionaceae, ericoid fynbos, wetland taxa, succulent and
 397 drought taxa, and Afrotemperate forest pollen percentages as well as of microcharcoal
 398 concentrations show persistent significant power within the 18–24 kyr precession

399 frequency bands (Figure 5). The same pattern is also found in the frequency analysis
400 of pollen concentrations and accumulation rates (Supplementary Figures 1 and 2).



401
402 **Figure 5.** REDFIT spectral analysis (window: hanning; oversample: 2; segments: 3) of the percentages
403 of different pollen groups and microcharcoal concentration from IODP Site U1479. Theor_AR_1_ means
404 theoretical first-order autoregressive (AR1). False-alarm levels of 80%, 90% and 95% are denoted.

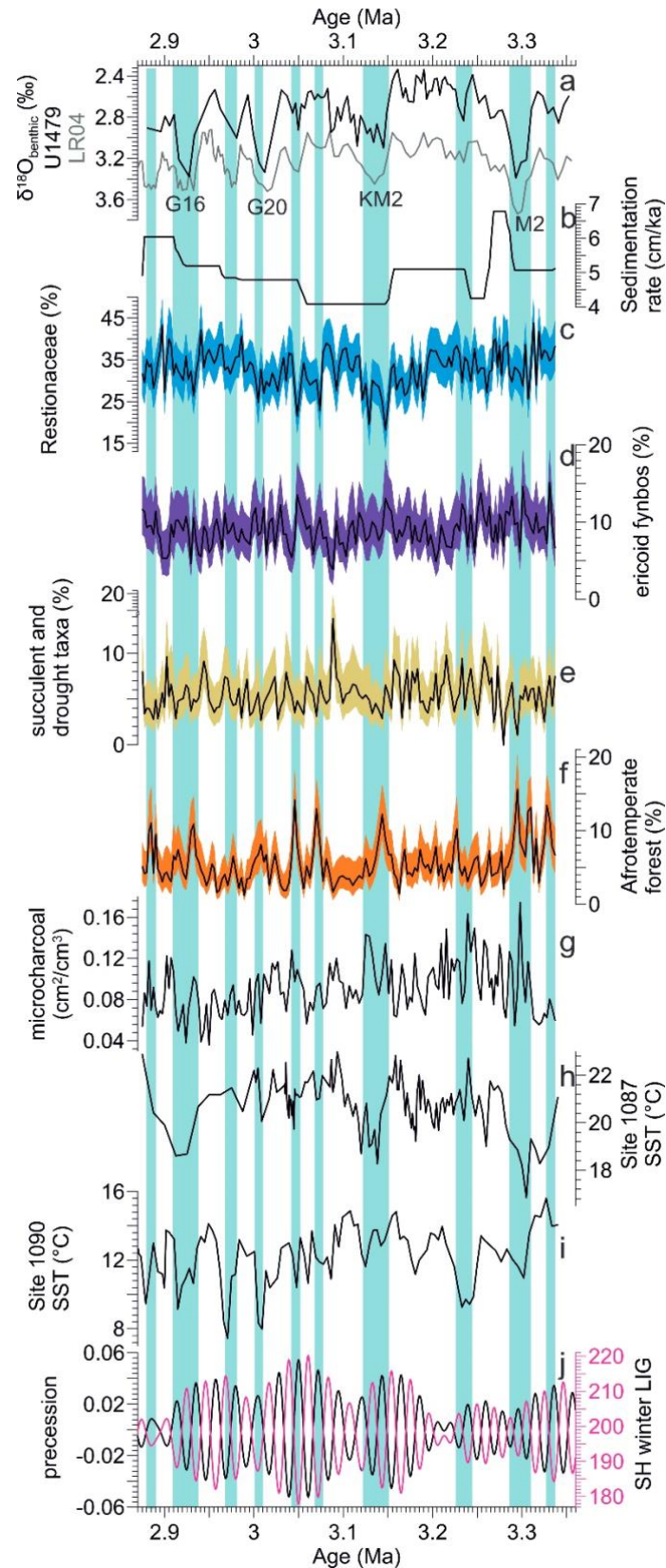
405 The benthic foraminifera $\delta^{18}\text{O}$ record shows characteristic 'glacial-interglacial' changes
406 similar to the global LR04 benthic $\delta^{18}\text{O}$ stack. The specific values are higher at Site
407 U1479. Several glacials including MIS M2, KM2, G20 and G16 correspond to the
408 minima of Restionaceae and maxima of ericoid fynbos taxa (Figure 6).

409 5. Discussion

410 5.1 Pollen transport and source area

411 Pollen and spores can be transported from the continent to the ocean either by wind
412 or by rivers. Although in the semi-arid regions of southwestern Africa, wind transport is
413 a major transport process for terrigenous material to the ocean (Prospero, 1981; Scott
414 and van Zinderen Barker, 1985), fluvial transport could also be possible. The Pliocene

415 pollen record at ODP Site 1082 (west of Namibia, Figure 2) indicates mixed fluvial and
416 aeolian pollen transport before 2.2 Ma (Dupont, 2006). Considering that southern
417 South Africa is predominantly influenced by southern westerlies and SE trade winds
418 throughout the year, however, direct wind transport of pollen from the Cape province
419 to Site U1479 seems unlikely as the study site is situated outside the direct influence
420 of the SE trade winds (Figure 2). Pollen and spores in sediments of Site U1479 are
421 more probably transported by the rivers of the Southern Cape in to the ocean and from
422 there by the strong Agulhas Current to the study site. This is supported by the
423 continuous presence of freshwater cyst *Pseudoschizaea* (Rossignol, 1962) in Site
424 U1479 (Figure 3). As previous studies indicate that fine grained, wind-blown
425 terrigenous material can travel as far as the Agulhas Ridge entrained within the
426 Agulhas Current (Petschick et al., 1996), we assume that pollen and spores can also
427 be transported and deposited here. The material of Site U1479 is relatively rich in
428 pollen and spores and the floral composition of the palynological assemblage
429 dominated by the family of Restionaceae clearly points to an origin in fynbos vegetation.
430 We presume, therefore, that the Agulhas Current is instrumental in the westward
431 transport of aeolian or fluvial pollen and spores reaching the ocean along south coast
432 of South Africa.



433

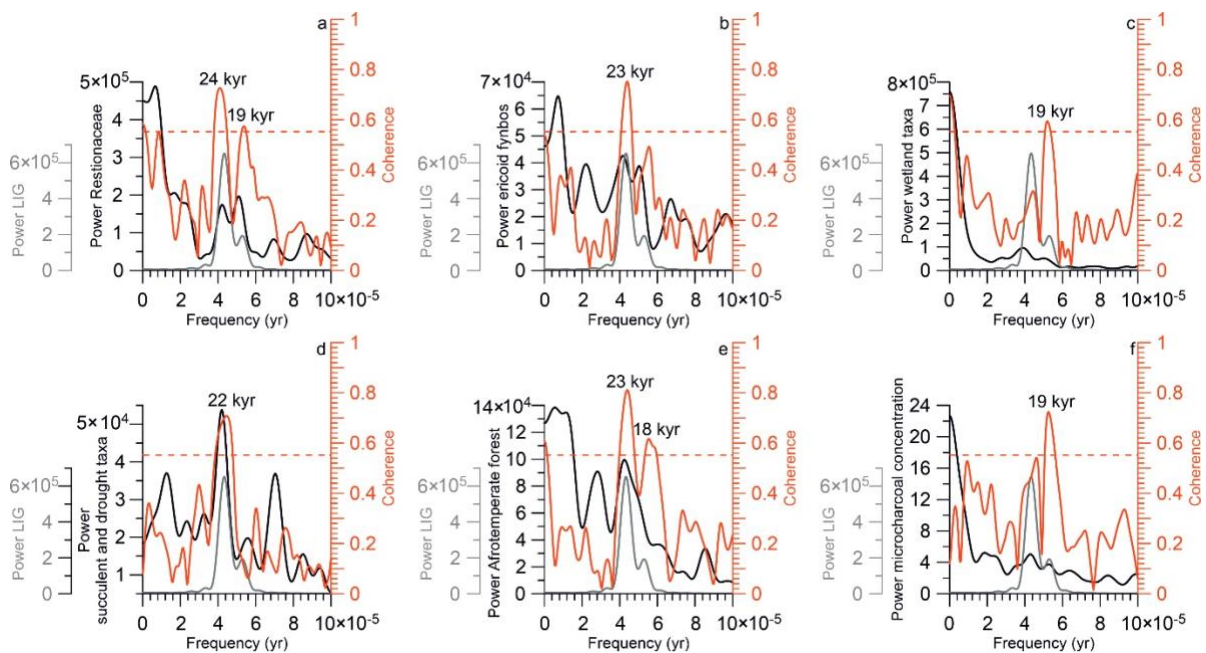
434 **Figure 6.** a) Oxygen isotopes of benthic foraminifera of IODP Site U1479 (black) compared to the global
 435 stack LR04 (gray) (Lisiecki and Raymo, 2005); b) sedimentation rates, c-f) pollen percentages and g)
 436 microcharcoal concentrations of IODP Site U1479; h-i) alkenone-derived SSTs from ODP Sites 1087

437 (Petrick et al., 2015, 2018) and 1090 (Martínez-García et al., 2010); j) precession (black) and southern
438 hemisphere latitudinal winter insolation gradient (LIG) (pink) (Laskar et al., 2004). Shadings of pollen
439 percentages denote 95% confidence intervals. The light blue vertical bars correspond to higher benthic
440 foraminifera $\delta^{18}\text{O}$ values, lower percentages of Restionaceae, high percentages of ericoid fynbos,
441 succulent and drought taxa and Afrotropical forest, higher values of microcharcoal concentrations in
442 IODP Site U1479 and colder SST in ODP Sites 1087 and 1090.

443 **5.2 Vegetation and hydroclimate response on latitudinal insolation** 444 **gradient forcing**

445 At IODP Site U1479, the late Pliocene is characterized by a long-term trend of
446 decrease prior to 3.147 Ma and after that an increase of both the percentage values
447 and accumulation rates of Restionaceae correspond to a decrease of Ericaceae values
448 (Figures 4 and 6). The maxima of both Restionaceae and ericoid fynbos taxa before
449 3.304 Ma indicate that fynbos was the dominant vegetation group in the Cape region,
450 suggesting wetter conditions. However, the general decreasing trend in both
451 percentages and accumulation rates of Restionaceae until 3.147 Ma suggests that that
452 the climate got drier. Pollen accumulation rates depend not only on the production of
453 pollen but also on the transport efficiency. On one hand, drier conditions could result
454 in a decline of vegetation cover leading to less pollen production. On the other hand, it
455 could result in decreased river discharge which might induce less terrestrial input to
456 our core site. This might explain the inverse trend of Cyperaceae, which starts from
457 minima at the beginning of the record and reaches maxima around 3.136 Ma.
458 Cyperaceae growing in wet habitats have an ambiguous relation to wetness. The
459 climate deterioration prior to 3.147 Ma might have caused drying of shallow lakes,
460 which then became wetlands leading to an increase of sedges. The drier conditions
461 are also implied by high microcharcoal concentrations until 3.239 Ma, suggesting an
462 increase in fire under more arid and seasonal conditions and a vegetation providing

463 enough fuel biomass (Daniau et al., 2013). After 3.239 Ma, a further decline of the
464 representation of Restionaceae was observed reaching a minimum at 3.147 Ma; at the
465 same time ericoid fynbos percentages increased to a maximum. This might suggest a
466 shift in the composition of the fynbos. According to Mucina and Rutherford (2006),
467 modern ericoid fynbos is the wettest type of fynbos. However, in this study, the shift to
468 ericoid fynbos appears to be associated with the onset of drier conditions, which is
469 supported by Valsecchi et al. (2013) who propose that ericoid fynbos is favored by drier
470 conditions and higher fire frequencies. The pollen assemblage of the late Pleistocene
471 inferred from the same site (IODP Site U1479) indicates a dramatic decrease in
472 Restionaceae pollen percentages (less than 30%) (unpublished results from Lydie
473 Dupont) in comparison to the pollen assemblage of the middle Pliocene (this study).
474 This suggests the existence of a no-analogue vegetation during the middle Pliocene.
475 The high representation of succulent and drought taxa between 3.273 and 3.156 Ma
476 also indicates relatively dry conditions. At a first glance, this interpretation seems to be
477 inconsistent with the minima in microcharcoal concentrations between 3.195 and 3.154
478 Ma indicating a decrease in fire frequencies. However, fires in southern Africa are
479 affected by the interaction of different factors such as the peak of the dry season, fuel
480 loads and rainfall seasonality (Daniau et al., 2013; Woillez et al., 2014). Additionally,
481 drier conditions resulting in decreased river discharge could also be responsible for
482 less transport of charcoal particles to the ocean. Considering the lower total pollen
483 accumulation rates between 3.239 and 3.059 Ma, the relatively low microcharcoal
484 concentrations are attributed to less fuel biomass and less terrestrial input into ocean.
485 From 3.147 Ma onwards, the increase of Restionaceae pollen percentages
486 accompanied with relatively high wetland taxa percentages, relatively low percentages
487 of ericoid fynbos pollen and succulent and drought taxa indicate a relative increase in
488 humidity.



489

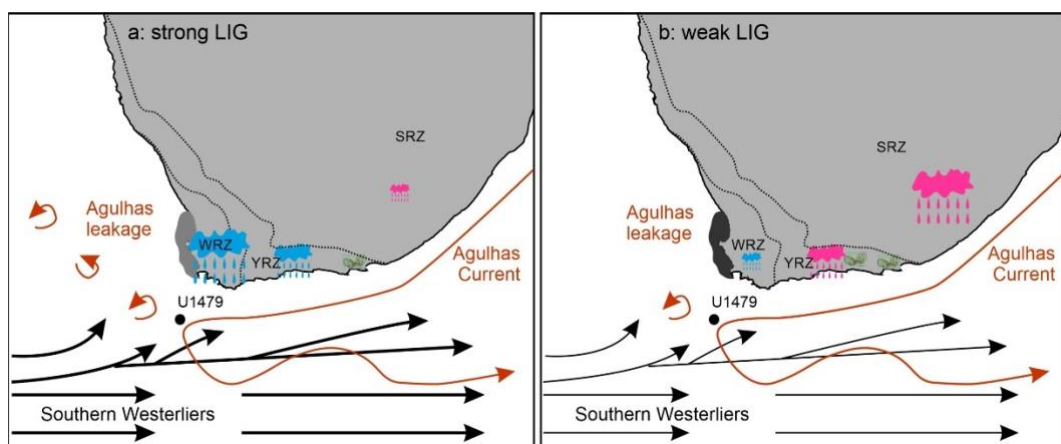
490 **Figure 7.** Cross spectral analysis between the percentages of different pollen groups (a, Restionaceae;
 491 b, ericoid fynbos; c, wetland taxa; d, succulent and drought taxa; e, Afrotemperate forest) and
 492 microcharcoal concentration (f) from IODP Site U1479 and LIG. The dash lines denote the non-zero
 493 coherence limit (values higher than 0.55 are significant at the 95% confidence interval).

494 On orbital and shorter timescales, we find general relationships among the records
 495 shown in Figure 6: pollen percentage minima of Restionaceae are associated with
 496 maxima of ericoid fynbos, succulent drought taxa, Afrotemperate forest and
 497 microcharcoal concentrations. Spectral analysis of the percentage values of
 498 Restionaceae, ericoid fynbos, succulent and drought taxa, and Afrotemperate forest
 499 as well as microcharcoal concentrations indicates significant periods of 18–24 kyr,
 500 suggesting a strong effect of precession (Figure 5). The results of cross spectral
 501 analysis support our interpretation indicating significant correlation between pollen
 502 groups and LIG at precession cycles (18-24 kyr) (Figure 7). Minima in Restionaceae
 503 occur in phase with maxima in precession and minima in LIG between 60 and 30°S of
 504 the southern hemisphere winter (21 June) (Supplementary Figure 3). Leads or lags
 505 occur in ericoid fynbos (lag of 9500 yr), wetland taxa (lag of 9500 yr), Succulent and

506 drought taxa (slight lead of 1400 yr), Afrotemperate forest (lead of 9200 yr at 23 kyr
507 cycle and 6100 at 18 kyr cycle) and microcharcoal concentration (lag of 8300 yr).

508 The dominance of precession cycles in the pollen signal might be the effect of the
509 latitudinal temperature gradient during the southern hemisphere winter approximated
510 by the LIG, which is important in the forcing of the climate in the winter rainfall regions
511 of the mid-latitudes (Davis and Brewer, 2009). A Holocene model climate study shows
512 that a weaker latitudinal temperature gradient leads to weaker mid-latitude westerly
513 flow, weaker cyclones and reduced mid-latitude precipitation (Routson et al., 2019). A
514 reduced equator-to-pole winter temperature gradient was also observed to be related
515 to a reduced equator-to-pole insolation gradient and reduced storm track activity over
516 the Mediterranean Sea using a high-resolution coupled climate mode (Bosmans et al.,
517 2015). A weak southern hemisphere winter gradient would weaken the southern
518 westerlies and reduce winter precipitation in both the WRZ and the YRZ (Figure 8).
519 Restionaceae, which have a strong winter-rainfall affiliation (Cowling et al., 1997),
520 decline due to the relatively dry conditions and reduced rainfall seasonality. Whereas,
521 in comparison to Restionaceae, ericoid fynbos is more favored by drier conditions.
522 Thus, the reduced winter precipitation and less Restionaceae will cause a relative
523 increase of ericoid fynbos. Based on pollen records, we could only refer that the relative
524 abundance of ericoid fynbos is higher which might be resulted from their areal extent.
525 The drier conditions also likely caused higher fire frequencies. The high-resolution
526 marine sediment core MD96-2098 off Namibia during the past 170,000 years in
527 southern Africa indicates high fire activity during precession maxima (Daniau et al.,
528 2013), which is well supported by the microcharcoal-based reconstructions of past fire
529 activity during MIS4 in southern Africa (Wouillez et al., 2014). In the YRZ, the high values
530 of Afrotemperate forest suggest more summer rainfall (Dupont et al., 2011; Quick et
531 al., 2018). Conversely a strong gradient would strengthen the westerlies and

532 associated rainfall in the WRZ and YRZ. Enhanced storm track activity of the southern
533 westerlies would result in humid conditions and intensified rainfall seasonality, leading
534 to high values of Restionaceae and lower values of ericoid fynbos as well as low fire
535 frequencies. A pollen and microcharcoal record from the coastal lake Eilandvlei shows
536 that the general long-term trend of increasing Afrotemperate forest with decreasing
537 fynbos was probably associated with reduced rainfall seasonality and more influences
538 of summer rainfall in maintaining higher moisture availability in the region (Quick et al.,
539 2018). Thus, in the YRZ, the intensified rainfall seasonality and more winter rainfall
540 would hamper the growth of Afrotemperate forest. The pollen record suggests a
541 response of the vegetation to trends in the average winter precipitation by variations in
542 the proportion of Ericaceae in the fynbos. Shifts between the amounts of winter and
543 summer rainfall in the YRZ influenced the development of Afrotemperate forest (Figure
544 6). In conclusion, we infer that the vegetation variation at the Cape region reflects
545 moisture variability during the mPWP which is related to the LIG in response to
546 precession forcing.



547
548 **Figure 8.** Conceptual model explaining the environmental variability for two different cases during the
549 mPWP in southern Africa. a) strong latitudinal insolation gradient (LIG) inducing strong southern
550 westerlies and warmer SST resulting from Antarctic sea ice retreat, stronger Agulhas leakage and/or
551 weakened upwelling. b) weak LIG inducing weak southern westerlies and cooler SST resulting from
552 Antarctic sea ice expansion, reduced Agulhas leakage and/or strengthened upwelling.

553 **5.3 Vegetation and hydroclimate response during glacials: forcing by**
554 **sea surface temperatures (SST)**

555 Even within the mPWP there are several glacials. In particular, the pronounced glacial
556 stage just before the onset of the mPWP known as “M2 glaciation” at 3.295 Ma in the
557 global stack LR04 $\delta^{18}\text{O}_{\text{benthics}}$ record (Lisiecki and Raymo, 2005) has been interpreted
558 as an early major global cooling event prior to the onset of the northern hemisphere
559 glaciations at ca. 2.6 Ma (De Schepper et al., 2009; Prell, 1984). A short interval with
560 lower values of Restionaceae and high values of ericoid fynbos as well as
561 Afrotemperate forest between 3.331 and 3.160 Ma was observed, which is broadly
562 coincident with this glacial MIS M2 (Figure 6). This is supported by the X-ray
563 Fluorescence (XRF) data from IODP Site U1478 off Limpopo which suggest increased
564 runoff during the MIS M2 in the Mozambique Channel probably related to increased
565 rainfall in the SRZ (Koutsodendris et al., 2020). However, the most pronounced period
566 in our pollen record occurs between 3.147 and 3.129 Ma when Restionaceae
567 percentages reach minima together with high values of ericoid fynbos (Figure 6). The
568 period corresponds to another glacial, MIS KM2, which is also considered to be one of
569 the pronounced glacials during the Pliocene (De Schepper et al., 2009). This is
570 supported by the high pollen percentage values of Ericaceae, which are often used as
571 an indicator of colder climate (Gasse and Van Campo, 1998; Scott, 1999). Apart from
572 these two glacials, there are several other glacials characterized by low percentage
573 values of Restionaceae, high percentage values of ericoid fynbos and Afrotemperate
574 forest in our pollen record. The glacials correspond well with cold SST recorded at
575 ODP Sites 1087 and 1090 (Figure 6) (Martínez-García et al., 2010; Petrick et al., 2015,
576 2018). The TEX₈₆ data from IODP Site U1478 off Limpopo also show a long-term SST
577 drop centered at ca. 3.2–3.1 Ma (Taylor et al., in review). We infer that SST influenced

578 hydroclimate variability and in turn vegetation during the mPWP. The colder SST would
579 reduce temperatures as well as winter rainfall in the WRZ and YRZ, which would lead
580 to a decline in Restionaceae and an increase in ericoid fynbos. The reduced
581 temperature and precipitation in the WRZ of southern Africa would thus enhance the
582 effect of weak winter LIG.

583 Numerical modelling supports our interpretation. Rreconstructed SST were simulated
584 and used to force a numerical climate model (Kamae et al., 2011). The results reveal
585 that wetter surface conditions in subtropical Africa during the mPWP are related to the
586 reduction of the meridional and zonal gradients of tropical SST rather than to orography,
587 land and/or sea ice. In this region, however, it is hard to distinguish between the
588 different factors resulting in variations of SST, which is affected by the interactions of
589 Agulhas leakage, Benguela Current as well as the advection of cold sub-Antarctic
590 water (Rosell-Melé et al., 2014).

591 Firstly, a decline in SST might be attributed to the global cooling triggered by Antarctic
592 ice sheet expansion. Proxy records and model studies generally infer a more northward
593 position of the southern westerlies during cooler climates/glacial periods (Bard and
594 Rickaby, 2009; Lamy et al., 2004; Williams and Bryan, 2006). A 800,000 year record
595 of SST and ocean productivity from marine sediment core MD96-2077 situated under
596 the Agulhas Current of the subtropical gyre of the Indian Ocean suggests a northward
597 shift of the southern westerlies by up to 7° of latitude during cooler stages (Bard and
598 Rickaby, 2009). This supports the model results of a 7° equatorward shift of the
599 subtropical fronts resulting from a global cooling of 3°C (Williams and Bryan, 2006).
600 The inference of weakened southern westerlies induced by the weak LIG during
601 glacials based on our pollen and microcharcoal records implies that there might be
602 some decoupling between the strength and the latitudinal position of the southern

603 westerlies. During glacials, northerly positioned southern westerlies might still show
604 fluctuations in strength.

605 Secondly, a decline in SST might be attributed to less Agulhas leakage. Previous
606 studies have shown that the northward shift of the southern westerlies during glacials
607 nearly shuts off the Agulhas leakage (Bard and Rickaby, 2009; Peeters et al., 2004).
608 The initial results of geochemical provenance studies on clays at our Site U1479
609 indicate reduced Agulhas leakage during the last glacial cycle and enhanced Agulhas
610 leakage during warmer periods (Franzese et al., 2018). The reconstructions of ice
611 sheet, SST and sea ice from an Antarctic sediment core showed that the intensification
612 of Antarctic cooling resulted in the expansion of southern westerlies and the northward
613 migration of ocean fronts in the Southern Ocean, which likely restricted the warm
614 Agulhas leakage (McKay et al., 2012). In this case, the low SST might be associated
615 with less Agulhas leakage influenced by the northward shift and weakened southern
616 westerlies during weak LIG. This is supported by the relatively cool SST and very low
617 abundances of Agulhas leakage indicator foraminifera (e.g., *Globigerina falconensis*
618 and *Globorotalia menardii*) at ODP Site 1087 suggesting an absence or weak influence
619 of Agulhas leakage during the mPWP (Petrick et al., 2015). The high representation of
620 Podocarpaceae during glacials in combination with restricted Agulhas leakage refutes
621 the idea of abundant Podocarpaceae pollen transport by the Agulhas Current from
622 southeastern South Africa. More likely, therefore, is that abundant pollen of
623 Podocarpaceae originated from Afrotemperate forest in the YRZ. Although it is widely
624 accepted that the southward shift of the southern westerlies would enable more
625 Agulhas leakage (Biajoch et al., 2009), the modeling study of Durgadoo et al. (2013)
626 emphasized that increased Agulhas leakage corresponds with increased intensity of
627 the southern westerlies, which would concur with our "strong LIG" case shown in
628 Figure 8.

629 Thirdly, a decline in SST might mark the switch from a warm to a cold mode of SE
630 trade wind-induced upwelling along the southwest African coast. Grain size data and
631 alkenone-based SST from sediment cores MD96-2086/87 located off Lüderitz (off
632 Namibia, SW Africa) indicate that the past long-term SST variations are primarily
633 induced by strengthened SE trade winds through intensified coastal upwelling
634 (Pichevin et al., 2005). The latest model results indicate intensification of upwelling of
635 colder waters in the Benguela Upwelling region during the Pleistocene resulting in
636 strongly lowered SST compared to the Pliocene, which is not simulated by global
637 models with a relatively coarse geographical resolution (Jung et al., 2014; Haywood et
638 al., 2020, accepted; McClymont et al., 2020). Although the upwelling was still weak
639 during the middle Pliocene, several studies have shown evidence of an upwelling
640 maximum in the southern Benguela system until ca. 2.8 Ma, which later progressed
641 northwards to its modern position offshore Lüderitz (Diekmann et al., 2003; Petrick et
642 al., 2015, 2018; Rommerskirchen et al., 2011). Fossil mollusc records from the west
643 coast of southern Africa indicate the existence of cold upwelling offshore south of 32°S
644 in the early Pleistocene (Tankard and Rogers, 1978). Alkenone-derived SST records
645 from the Agulhas Basin to the northern Benguela system indicate different patterns of
646 SST since 5 Ma (Etourneau et al., 2009; Martínez-García et al., 2010; Petrick et al.,
647 2015, 2018; Rommerskirchen et al., 2011; Rosell-Melé et al., 2014), suggesting
648 upwelling was controlled by different processes in the southern and northern Benguela
649 system. This is for instance supported by the absence of cold SST in the northern
650 Benguela system (ODP Sites 1084, 1082 and 1081) during the glacials MIS M2 and
651 KM2 (Petrick et al., 2015). Multiproxy studies suggest more extensive upwelling in the
652 southern Benguela system during the mPWP (Petrick et al., 2015). The global cooling
653 with increased Antarctic glaciations promoting intermediate and bottom water
654 formation combined with intensified SE trade winds (intensified Hadley circulation) and

655 uplift of East Africa would have caused intensified upwelling offshore of southern Africa
656 (Etourneau et al., 2009; Jung et al., 2014; Marlow et al., 2000; Rommerskirchen et al.,
657 2011; Rosell-Melé et al., 2014). In our "weak LIG" case, the weakened southern
658 westerlies combined with strong SE trade winds would cause intensified upwelling,
659 resulting in cold water conditions over our core site and less rainfall in the WRZ.
660 Whereas in the "strong LIG" case, the strong southern westerlies and weak SE trade
661 winds would cause weakened upwelling (Figure 8).

662 **6 Conclusions**

663 The development of vegetation and climate in southwestern South Africa during the
664 mid-Piacenzian have been documented in detail by pollen, microcharcoal and benthic
665 foraminifera oxygen isotope records from marine sediment cores of IODP Site U1479
666 retrieved from the Cape Basin offshore of South Africa covering the period from 3.337
667 to 2.875 Ma.

668 Pollen assemblages throughout the record are characterized by the family of
669 Restionaceae indicating a clear pollen source from fynbos vegetation during the
670 mPWP. Variations in the representation of Restionaceae, ericoid fynbos and
671 Afrotemperate forest show dominant precession cycles indicating influence by the
672 latitudinal insolation gradient (LIG) in response to precession forcing. The weak/strong
673 southern hemisphere winter gradient would weaken/strengthen the southern
674 westerlies and winter precipitation in the WRZ and YRZ as well as influence the relative
675 amounts between winter and summer rainfall in the YRZ.

676 The glacial events reflected by the benthic foraminifera oxygen isotope record
677 correspond well with cooler SE Atlantic sea surface temperatures (SST) off South
678 Africa and are consistent with the vegetation and hydroclimate variability deduced from
679 our pollen and microcharcoal records. The cooler SST inducing less rainfall in the

680 winter rainfall zone, were likely driven by interactions of both atmospheric and
681 oceanographic processes including Antarctic ice sheet expansion, less contribution of
682 the Agulhas leakage and/or intensified southern Benguela upwelling.

683 On the basis of our study and comparisons with published records offshore of
684 southwestern Africa, we propose that LIG forcing (precession) and SST forcing were
685 the main drivers of hydroclimate in southwestern South Africa during the mPWP.
686 During “weak LIG”, the weakened southern westerlies combined with cold SST result
687 in less rainfall in the WRZ, while during “strong LIG”, the strong southern westerlies
688 together with warm SST would bring more rainfall in the WRZ.

689 **Acknowledgments**

690 This study was financially supported by the International Ocean Discovery Program,
691 IODP (SPP527) of the Deutsche Forschungsgemeinschaft (DFG), grant Nr. DU221/7.
692 Thibaut Caley is supported by CNRS-INSU. Funding from IODP France and LEFE
693 IMAGO CNRS INSU project SeaSalt are acknowledged. We thank the Captain, officers,
694 crew and especially all scientists sailing on IODP expedition 361. Thanks to Jutta
695 Scheffing for assistance with the pollen sample preparations in the lab. We would like
696 to thank the two reviewers for their helpful and constructive comments that have helped
697 to improve the manuscript.

698 **References**

- 699 Bard, E., Rickaby, R.E., 2009. Migration of the subtropical front as a modulator of glacial
700 climate. *Nature* 460, 380-383, <https://doi.org/10.1038/nature08189>.
- 701 Bergh, N.G., Verboom, G., Rouget, M., Cowling, R.M., 2014. Vegetation types of the greater
702 cape floristic region, in: Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), *Fynbos: Ecology, evolution, and conservation of a megadiverse region*. Oxford University Press.
703 <https://doi.org/10.1093/acprof:oso/9780199679584.003.0001>.
- 704

705 Biastoch, A., Böning, C.W., Schwarzkopf, F.U., Lutjeharms, J., 2009. Increase in Agulhas
706 leakage due to poleward shift of Southern Hemisphere westerlies. *Nature* 462, 495-
707 498, <https://doi.org/10.1038/nature08519>.

708 Bond, W., 1996. Fire, in: Cowling, R., Richardson, D., Pierce, S. (Eds.), *The vegetation of*
709 *southern Africa*. Cambridge University Press: Cambridge, pp. 421-446.

710 Bonnefille, R., Riollet, G., 1980. *Pollen des savanes d'Afrique orientale*. Éditions du Centre
711 national de la recherche scientifique, Paris.

712 Bosmans, J., Drijfhout, S., Tuenter, E., Hilgen, F., Lourens, L.J., Rohling, E., 2015. Precession
713 and obliquity forcing of the freshwater budget over the Mediterranean. *Quaternary*
714 *Science Reviews* 123, 16-30, <http://dx.doi.org/10.1016/j.quascirev.2015.06.008>.

715 Burls, N.J., Fedorov, A.V., 2017. Wetter subtropics in a warmer world: Contrasting past and
716 future hydrological cycles. *Proceedings of the National Academy of Sciences* 114,
717 12888-12893, <https://doi.org/10.1073/pnas.1703421114>.

718 Carr, A.S., Boom, A., Grimes, H.L., Chase, B.M., Meadows, M.E., Harris, A., 2014. Leaf wax
719 n-alkane distributions in arid zone South African flora: Environmental controls,
720 chemotaxonomy and palaeoecological implications. *Organic Geochemistry* 67, 72-84,
721 <https://doi.org/10.1016/j.orggeochem.2013.12.004>.

722 Chase, B.M., Meadows, M.E., 2007. Late Quaternary dynamics of southern Africa's winter
723 rainfall zone. *Earth-Science Reviews* 84, 103-138,
724 <https://doi.org/10.1016/j.earscirev.2007.06.002>.

725 Clark, R.L., 1982. Point count estimation of charcoal in pollen preparations and thin sections
726 of sediments. *Pollen et spores* 24, 23-35.

727 Cowling, R.M., Richardson, D.M., Pierce, S.M., 1997. *Vegetation of southern Africa*.
728 Cambridge University Press, Cambridge.

729 Crowley, T.J., 1996. Pliocene climates: the nature of the problem. *Marine Micropaleontology*
730 27, 3-12, [https://doi.org/10.1016/0377-8398\(95\)00049-6](https://doi.org/10.1016/0377-8398(95)00049-6).

731 Daniau, A.-L., Sánchez Goñi, M.F., Martinez, P., Urrego, D.H., Bout-Roumazielles, V., Desprat,
732 S., Marlon, J.R., 2013. Orbital-scale climate forcing of grassland burning in southern

733 Africa. Proceedings of the National Academy of Sciences 110, 5069-5073,
734 <https://doi.org/10.1073/pnas.1214292110>.

735 Davis, B.A.S., Brewer, S., 2009. Orbital forcing and role of the latitudinal insolation/temperature
736 gradient. *Climate Dynamics* 32, 143-165, <https://doi.org/10.1007/s00382-008-0480-9>.

737 De Schepper, S., Head, M.J., Groeneveld, J., 2009. North Atlantic Current variability through
738 marine isotope stage M2 (circa 3.3 Ma) during the mid-Pliocene. *Paleoceanography* 24,
739 <https://doi.org/10.1029/2008pa001725>.

740 Diekmann, B., Fälker, M., Kuhn, G., 2003. Environmental history of the south-eastern South
741 Atlantic since the Middle Miocene: evidence from the sedimentological records of ODP
742 Sites 1088 and 1092. *Sedimentology* 50, 511-529, <https://doi.org/10.1046/j.1365-3091.2003.00562.x>.

744 Dolan, A.M., Haywood, A.M., Hill, D.J., Dowsett, H.J., Hunter, S.J., Lunt, D.J., Pickering, S.J.,
745 2011. Sensitivity of Pliocene ice sheets to orbital forcing. *Palaeogeography,*
746 *Palaeoclimatology,* *Palaeoecology* 309, 98-110,
747 <https://doi.org/10.1016/j.palaeo.2011.03.030>.

748 Dowsett, H.J., Cronin, T.M., Poore, R.Z., Thompson, R.S., Whatley, R.C., Wood, A.M., 1992.
749 Micropaleontological Evidence for Increased Meridional Heat Transport in the North
750 Atlantic Ocean During the Pliocene. *Science* 258, 1133-1135.
751 <https://doi.org/10.1126/science.258.5085.1133>.

752 Dupont, L.M., 2006. Late Pliocene vegetation and climate in Namibia (southern Africa) derived
753 from palynology of ODP Site 1082. *Geochemistry, Geophysics, Geosystems* 7,
754 <https://doi.org/10.1029/2005gc001208>.

755 Dupont, L.M., Linder, H.P., Rommerskirchen, F., Schefuß, E., 2011. Climate-driven rampant
756 speciation of the Cape flora. *Journal of Biogeography* 38, 1059-1068,
757 <https://doi.org/10.1111/j.1365-2699.2011.02476.x>.

758 Durgadoo, J.V., Loveday, B.R., Reason, C.J., Penven, P., Biastoch, A., 2013. Agulhas leakage
759 predominantly responds to the Southern Hemisphere westerlies. *Journal of Physical*
760 *Oceanography* 43, 2113-2131, <https://doi.org/10.1175/JPO-D-13-047.1>.

761 Eckardt, F., Kuring, N., 2005. SeaWiFS identifies dust sources in the Namib Desert.
762 International Journal of Remote Sensing 26, 4159-4167,
763 <https://doi.org/10.1080/01431160500113112>.

764 Engelbrecht, C.J., Landman, W.A., Engelbrecht, F.A., Malherbe, J., 2015. A synoptic
765 decomposition of rainfall over the Cape south coast of South Africa. *Climate Dynamics*
766 44, 2589-2607, <https://doi.org/10.1007/s00382-014-2230-5>.

767 Etourneau, J., Martinez, P., Blanz, T., Schneider, R., 2009. Pliocene–Pleistocene variability of
768 upwelling activity, productivity, and nutrient cycling in the Benguela region. *Geology* 37,
769 871-874, <https://doi.org/10.1130/g25733a.1>.

770 Franzese, A.M., Hemming, S.R., Pearson, B., Kafando, O., Sinadinse, A., 2018. Assessing
771 Agulhas Leakage using Terrigenous Sediment Provenance at IODP Site U1479: Initial
772 Results, AGU Fall Meeting Abstracts.

773 Gasse, F., Van Campo, E., 1998. A 40,000-yr pollen and diatom record from Lake Tritrivakely,
774 Madagascar, in the southern tropics. *Quaternary Research* 49, 299-311,
775 <https://doi.org/10.1006/qres.1998.1967>.

776 Goldblatt, P., Manning, J.C., 2002. Plant diversity of the Cape region of southern Africa. *Annals*
777 *of the Missouri Botanical Garden*, 281-302, <https://doi.org/10.2307/3298566>.

778 Grimm, E., 2015. Tilia and TGView 19 version 2.0. 41. software. Springfield, USA: Illinois State
779 Museum, Research and Collection Center.

780 Hall, I., Hemming, S., LeVay, L., Barker, S., Berke, M., Brentegani, L., Caley, T., Cartagena-
781 Sierra, A., Charles, C., Coenen, J., 2017. Site U1479, Proceedings of the International
782 Ocean Discovery Program, 361. International Ocean Discovery Program.

783 Hammer, Ø., Harper, D.A., Ryan, P.D., 2001. PAST: Paleontological statistics software
784 package for education and data analysis. *Palaeontologia electronica* 4, 9.

785 Haywood, A.M., Dowsett, H.J., Valdes, P.J., Lunt, D.J., Francis, J.E., Sellwood, B.W., 2009.
786 Introduction. Pliocene climate, processes and problems. *Philosophical Transactions of*
787 *the Royal Society A: Mathematical, Physical and Engineering Sciences* 367, 3-17,
788 <https://doi.org/10.1098/rsta.2008.0205>.

789 Haywood, A.M., Hill, D.J., Dolan, A.M., Otto-Bliesner, B.L., Bragg, F., Chan, W.L., Chandler,
790 M.A., Contoux, C., Dowsett, H.J., Jost, A., Kamae, Y., Lohmann, G., Lunt, D.J., Abe-
791 Ouchi, A., Pickering, S.J., Ramstein, G., Rosenbloom, N.A., Salzmann, U., Sohl, L.,
792 Stepanek, C., Ueda, H., Yan, Q., Zhang, Z., 2013. Large-scale features of Pliocene
793 climate: results from the Pliocene Model Intercomparison Project. *Climate of the Past*
794 9, 191-209, <https://doi.org/10.5194/cp-9-191-2013>.

795 Haywood, A.M., Tindall, J.C., Dowsett, H.J., Dolan, A.M., Foley, K.M., Hunter, S.J., Hill, D.J.,
796 Chan, W.L., Abe-Ouchi, A., Stepanek, C., Lohmann, G., Chandan, D., Peltier, W.R.,
797 Tan, N., Contoux, C., Ramstein, G., Li, X., Zhang, Z., Guo, C., Nisancioglu, K.H., Zhang,
798 Q., Li, Q., Kamae, Y., Chandler, M.A., Sohl, L.E., Otto-Bliesner, B.L., Feng, R., Brady,
799 E.C., von der Heydt, A.S., Baatsen, M.L.J., Lunt, D.J., 2020. A return to large-scale
800 features of Pliocene climate: the Pliocene Model Intercomparison Project Phase 2.
801 *Climate of the Past Discuss.* 2020, 1-40, <https://doi.org/10.5194/cp-2019-145>.

802 Haywood, A.M., Valdes, P.J., 2004. Modelling Pliocene warmth: contribution of atmosphere,
803 oceans and cryosphere. *Earth and Planetary Science Letters* 218, 363-377,
804 [https://doi.org/10.1016/S0012-821X\(03\)00685-X](https://doi.org/10.1016/S0012-821X(03)00685-X).

805 Hijmans, R., Cameron, S., Parra, J., Jones, P., Jarvis, A., Richardson, K., 2005. WorldClim,
806 version 1.3, University of California, Berkeley.

807 Hunter, S.J., Haywood, A.M., Dolan, A.M., Tindall, J.C., 2019. The HadCM3 contribution to
808 PlioMIP phase 2. *Climate of the Past* 15, 1691-1713, [https://doi.org/10.5194/cp-15-](https://doi.org/10.5194/cp-15-1691-2019)
809 1691-2019.

810 Jung, G., Prange, M., Schulz, M., 2014. Uplift of Africa as a potential cause for Neogene
811 intensification of the Benguela upwelling system. *Nature Geoscience* 7, 741-747,
812 <https://doi.org/10.1038/ngeo2249>.

813 Kamae, Y., Ueda, H., Kitoh, A., 2011. Hadley and Walker circulations in the mid-Pliocene warm
814 period simulated by an atmospheric general circulation model. *Journal of the*
815 *Meteorological Society of Japan. Ser. II* 89, 475-493, [https://doi.org/10.2151/jmsj.2011-](https://doi.org/10.2151/jmsj.2011-505)
816 505.

817 Koutsodendris, A., Nakajima, K., Kaboth-Bahr, S., Berke, M.A., Franzese, A.M., Hall, I.R.,
818 Hemming, S.R., Just, J., LeVay, L.J., Pross, J., Robinson, R., and IODP Expedition 361
819 scientists, 2020: A Plio-Pleistocene (c. 0 – 4 Ma) cyclostratigraphy for IODP Site U1478
820 (Mozambique Channel, SW Indian Ocean): Exploring an offshore record of
821 paleoclimate and ecosystem variability in SE Africa. *Newsletters on Stratigraphy*,
822 <https://doi.org/10.1127/nos/2020/0608>.

823 Lamy, F., Kaiser, J., Ninnemann, U., Hebbeln, D., Arz, H.W., Stoner, J., 2004. Antarctic timing
824 of surface water changes off Chile and Patagonian ice sheet response. *Science* 304,
825 1959-1962, <https://doi.org/10.1126/science.1097863>.

826 Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A.C.M., Levrard, B., 2004. A long-
827 term numerical solution for the insolation quantities of the Earth. *A&A* 428, 261-285,
828 <https://doi.org/10.1051/0004-6361:20041335>.

829 Lau, W.K.M., Wu, H.T., Kim, K.M., 2013. A canonical response of precipitation characteristics
830 to global warming from CMIP5 models. *Geophysical Research Letters* 40, 3163-3169,
831 <https://doi.org/10.1002/grl.50420>.

832 Levin, N.E., 2015. Environment and climate of early human evolution. *Annual Review of Earth*
833 *and Planetary Sciences* 43, 405-429, [https://doi.org/10.1146/annurev-earth-060614-](https://doi.org/10.1146/annurev-earth-060614-105310)
834 [105310](https://doi.org/10.1146/annurev-earth-060614-105310).

835 Linder, H.P., 2003. The radiation of the Cape flora, southern Africa. *Biological Reviews* 78,
836 597-638, <https://doi.org/10.1017/s1464793103006171>.

837 Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed
838 benthic $\delta^{18}\text{O}$ records. *Paleoceanography* 20, <https://doi.org/10.1029/2004pa001071>.

839 Lunt, D.J., Haywood, A.M., Schmidt, G.A., Salzmann, U., Valdes, P.J., Dowsett, H.J., Loptson,
840 C.A., 2012. On the causes of mid-Pliocene warmth and polar amplification. *Earth and*
841 *Planetary Science Letters* 321, 128-138, <https://doi.org/10.1016/j.epsl.2011.12.042>.

842 Maher, L.J., 1972. Nomograms for computing 0.95 confidence limits of pollen data. *Review of*
843 *Palaeobotany and Palynology* 13, 85-93, [http://dx.doi.org/10.1016/0034-](http://dx.doi.org/10.1016/0034-6667(72)90038-3)
844 [6667\(72\)90038-3](http://dx.doi.org/10.1016/0034-6667(72)90038-3).

845 Marchitto, T., Curry, W., Lynch-Stieglitz, J., Bryan, S., Cobb, K., Lund, D., 2014. Improved
846 oxygen isotope temperature calibrations for cosmopolitan benthic foraminifera.
847 *Geochimica et Cosmochimica Acta* 130, 1-11,
848 <https://doi.org/10.1016/j.gca.2013.12.034>.

849 Martin, H., 2006. Cenozoic climatic change and the development of the arid vegetation in
850 Australia. *Journal of Arid Environments* 66, 533-563,
851 <https://doi.org/10.1016/j.jaridenv.2006.01.009>.

852 Martínez-García, A., Rosell-Melé, A., McClymont, E.L., Gersonde, R., Haug, G.H., 2010.
853 Subpolar Link to the Emergence of the Modern Equatorial Pacific Cold Tongue. *Science*
854 328, 1550-1553, <https://doi.org/10.1126/science.1184480>.

855 McClymont, E.L., Ford, H.L., Ho, S.L., Tindall, J.C., Haywood, A.M., Alonso-Garcia, M., Bailey,
856 I., Berke, M.A., Littler, K., Patterson, M.O., Petrick, B., Peterse, F., Ravelo, A.C.,
857 Risebrobakken, B., De Schepper, S., Swann, G.E.A., Thirumalai, K., Tierney, J.E., van
858 der Weijst, C., White, S., Abe-Ouchi, A., Baatsen, M.L.J., Brady, E.C., Chan, W.L.,
859 Chandan, D., Feng, R., Guo, C., von der Heydt, A.S., Hunter, S., Li, X., Lohmann, G.,
860 Nisancioglu, K.H., Otto-Bliesner, B.L., Peltier, W.R., Stepanek, C., Zhang, Z., 2020.
861 Lessons from a high-CO₂ world: an ocean view from ~ 3 million years ago. *Climate of*
862 *the Past* 16, 1599-1615, <https://doi.org/10.5194/cp-16-1599-2020>.

863 McKay, R., Naish, T., Carter, L., Riesselman, C., Dunbar, R., Sjunneskog, C., Winter, D.,
864 Sangiorgi, F., Warren, C., Pagani, M., Schouten, S., Willmott, V., Levy, R., DeConto,
865 R., Powell, R.D., 2012. Antarctic and Southern Ocean influences on Late Pliocene
866 global cooling. *Proceedings of the National Academy of Sciences* 109, 6423-6428,
867 <https://doi.org/10.1073/pnas.1112248109>.

868 Mucina, L., Rutherford, M.C., 2006. *The Vegetation of South Africa, Lesotho and Swaziland*.
869 South African National Biodiversity Institute.

870 Nelson, G., Hutchings, L., 1983. The Benguela upwelling area. *Progress in Oceanography* 12,
871 333-356, [http://dx.doi.org/10.1016/0079-6611\(83\)90013-7](http://dx.doi.org/10.1016/0079-6611(83)90013-7).

872 Pagani, M., Liu, Z., LaRiviere, J., Ravelo, A.C., 2010. High Earth-system climate sensitivity
873 determined from Pliocene carbon dioxide concentrations. *Nature Geoscience* 3, 27-30,
874 <https://doi.org/10.1038/ngeo724>.

875 Paillard, D., Labeyrie, L., Yiou, P., 1996. AnalySeries 1.0: a Macintosh software for the analysis
876 of geophysical time-series. *Eos* 77, 379.

877 Peeters, F.J.C., Acheson, R., Brummer, G.-J.A., de Ruijter, W.P.M., Schneider, R.R., Ganssen,
878 G.M., Ufkes, E., Kroon, D., 2004. Vigorous exchange between the Indian and Atlantic
879 oceans at the end of the past five glacial periods. *Nature* 430, 661-665,
880 <http://dx.doi.org/10.1038/nature02785>.

881 Petrick, B., McClymont, E.L., Felder, S., Rueda, G., Leng, M.J., Rosell-Melé, A., 2015. Late
882 Pliocene upwelling in the Southern Benguela region. *Palaeogeography,*
883 *Palaeoclimatology, Palaeoecology* 429, 62-71,
884 <https://doi.org/10.1016/j.palaeo.2015.03.042>.

885 Petrick, B., McClymont, E.L., Littler, K., Rosell-Melé, A., Clarkson, M.O., Maslin, M., Röhl, U.,
886 Shevenell, A.E., Pancost, R.D., 2018. Oceanographic and climatic evolution of the
887 southeastern subtropical Atlantic over the last 3.5 Ma. *Earth and Planetary Science*
888 *Letters* 492, 12-21, <https://doi.org/10.1016/j.epsl.2018.03.054>.

889 Petschick, R., Kuhn, G., Gingele, F., 1996. Clay mineral distribution in surface sediments of
890 the South Atlantic: sources, transport, and relation to oceanography. *Marine Geology*
891 130, 203-229, [https://doi.org/10.1016/0025-3227\(95\)00148-4](https://doi.org/10.1016/0025-3227(95)00148-4).

892 Pichevin, L., Cremer, M., Giraudeau, J., Bertrand, P., 2005. A 190 ky record of lithogenic grain-
893 size on the Namibian slope: Forging a tight link between past wind-strength and coastal
894 upwelling dynamics. *Marine Geology* 218, 81-96,
895 <https://doi.org/10.1016/j.margeo.2005.04.003>.

896 Prell, W.L., 1984. Covariance Patterns of Foraminiferal $\delta^{18}O$: An Evaluation of Pliocene Ice
897 Volume Changes Near 3.2 Million Years Ago. *Science* 226, 692-694,
898 <https://doi.org/10.1126/science.226.4675.692>.

899 Prescott, C.L., Dolan, A.M., Haywood, A.M., Hunter, S.J., Tindall, J.C., 2018. Regional climate
900 and vegetation response to orbital forcing within the mid-Pliocene Warm Period: A
901 study using HadCM3. *Global and Planetary Change* 161, 231-243,
902 <https://doi.org/10.1016/j.gloplacha.2017.12.015>.

903 Prospero, J., 1981. Aeolian transport to the world ocean, in: Emiliani, C. (Ed.), *The sea*, vol. 7,
904 *The oceanic lithosphere*. Wiley Interscience, New York, pp. 801-874.

905 Quick, L.J., Chase, B.M., Wündsche, M., Kirsten, K.L., Chevalier, M., Mäusbacher, R.,
906 Meadows, M.E., Haberzettl, T., 2018. A high-resolution record of Holocene climate and
907 vegetation dynamics from the southern Cape coast of South Africa: pollen and
908 microcharcoal evidence from Eilandvlei. *Journal of Quaternary Science* 33, 487-500,
909 <https://doi.org/10.1002/jqs.3028>.

910 Raymo, M.E., Grant, B., Horowitz, M., Rau, G.H., 1996. Mid-Pliocene warmth: stronger
911 greenhouse and stronger conveyor. *Marine Micropaleontology* 27, 313-326,
912 [https://doi.org/10.1016/0377-8398\(95\)00048-8](https://doi.org/10.1016/0377-8398(95)00048-8).

913 Raymo, M.E., Mitrovica, J.X., O'Leary, M.J., DeConto, R.M., Hearty, P.J., 2011. Departures
914 from eustasy in Pliocene sea-level records. *Nature Geoscience* 4, 328-332,
915 <https://doi.org/10.1038/ngeo1118>.

916 Rind, D., Chandler, M., 1991. Increased ocean heat transports and warmer climate. *Journal of*
917 *Geophysical Research: Atmospheres* 96, 7437-7461.
918 <https://doi.org/10.1029/91jd00009>.

919 Rommerskirchen, F., Condon, T., Mollenhauer, G., Dupont, L., Schefuss, E., 2011. Miocene
920 to Pliocene development of surface and subsurface temperatures in the Benguela
921 Current system. *Paleoceanography* 26, <https://doi.org/10.1029/2010pa002074>.

922 Rosell-Melé, A., Martínez-García, A., McClymont, E.L., 2014. Persistent warmth across the
923 Benguela upwelling system during the Pliocene epoch. *Earth and Planetary Science*
924 *Letters* 386, 10-20, <https://doi.org/10.1016/j.epsl.2013.10.041>.

925 Rossignol, M., 1962. Analyse pollinique de sédiments marins quaternaires en Israël II. -
926 Sédiments pleistocènes. *Pollen et Spores* 4, 121-148.

927 Routson, C.C., McKay, N.P., Kaufman, D.S., Erb, M.P., Goose, H., Shuman, B.N., Rodysill,
928 J.R., Ault, T., 2019. Mid-latitude net precipitation decreased with Arctic warming during
929 the Holocene. *Nature* 568, 83-87, <https://doi.org/10.1038/s41586-019-1060-3>.

930 Salzmann, U., Haywood, A.M., Lunt, D.J., Valdes, P.J., Hill, D.J., 2008. A new global biome
931 reconstruction and data-model comparison for the Middle Pliocene. *Global Ecology and*
932 *Biogeography* 17, 432-447, <https://doi.org/10.1111/j.1466-8238.2008.00381.x>.

933 Schulz, M., Mudelsee, M., 2002. REDFIT: estimating red-noise spectra directly from unevenly
934 spaced paleoclimatic time series. *Computers & Geosciences* 28, 421-426,
935 [https://doi.org/10.1016/S0098-3004\(01\)00044-9](https://doi.org/10.1016/S0098-3004(01)00044-9).

936 Scott, L., 1982. Late Quaternary fossil pollen grains from the Transvaal, South Africa. *Review*
937 *of Palaeobotany and Palynology* 36, 241-278, [https://doi.org/10.1016/0034-](https://doi.org/10.1016/0034-6667(82)90022-7)
938 [6667\(82\)90022-7](https://doi.org/10.1016/0034-6667(82)90022-7).

939 Scott, L., 1999. Vegetation history and climate in the Savanna biome South Africa since
940 190,000 ka: a comparison of pollen data from the Tswaing Crater (the Pretoria Saltpan)
941 and Wonderkrater. *Quaternary International* 57, 215-223,
942 [https://doi.org/10.1016/S1040-6182\(98\)00062-7](https://doi.org/10.1016/S1040-6182(98)00062-7).

943 Scott, L., Partridge, T., 1994. Some manifestations of Pliocene warming in southern Africa, in:
944 Thompson, R.S. (Ed.), *Pliocene Terrestrial Environments and Data/Model*
945 *Comparisons*. US Geological Survey Open-File Report 94-23, pp. 54-55.

946 Scott, L., van Zinderen Barker, S.E., 1985. Exotic pollen and long-distance wind dispersal at a
947 sub-Antarctic Island. *Grana* 24, 45-54. <https://doi.org/10.1080/00173138509427422>.

948 Shannon, L.V., Nelson, G., 1996. The Benguela: large scale features and processes and
949 system variability, in: Wefer, G., Berger, W.H., Siedler, G., Webb, D. (Eds.), *The South*
950 *Atlantic: Present and Past Circulation*. Springer-Verlag, Berlin Heidelberg, pp. 63-210.

951 Tankard, A.J., Rogers, J., 1978. Late Cenozoic Palaeoenvironments on the West Coast of
952 Southern Africa. *Journal of Biogeography* 5, 319-337, <https://doi.org/10.2307/3038026>.

953 Tyson, P.D., Preston-Whyte, R.A., 2000. *The weather and climate of southern Africa*. Oxford
954 University Press, Cape Town.

955 Valsecchi, V., Chase, B.M., Slingsby, J.A., Carr, A.S., Quick, L.J., Meadows, M.E., Cheddadi,
956 R., Reimer, P.J., 2013. A high resolution 15,600-year pollen and microcharcoal record
957 from the Cederberg Mountains, South Africa. *Palaeogeography, Palaeoclimatology,*
958 *Palaeoecology* 387, 6-16, <https://doi.org/10.1016/j.palaeo.2013.07.009>.

959 Van As, J., du Preez, J., Brown, L., Smit, N., 2012. *The Story of Life & the Environment.*
960 Penguin Random House South Africa.

961 Wheeler, A.D., 2010. *Impacts of degradation on critically endangered Oudtshoorn Gannaveld.*
962 University of the Western Cape, Cape Town, South Africa.

963 Williams, G.P., Bryan, K., 2006. Ice age winds: An aquaplanet model. *Journal of climate* 19,
964 1706-1715, <https://doi.org/10.1175/JCLI3766.1>.

965 Woillez, M.-N., Levavasseur, G., Daniau, A.-L., Kageyama, M., Urrego, D., Sánchez-Goñi, M.-
966 F., Hanquiez, V., 2014. Impact of precession on the climate, vegetation and fire activity
967 in southern Africa during MIS4. *Climate of the Past* 10, 1165-1182,
968 <https://doi.org/10.5194/cp-10-1165-2014>.

969 Zhao, X., Dupont, L., Meadows, M.E., Wefer, G., 2016a. Pollen distribution in the marine
970 surface sediments of the mudbelt along the west coast of South Africa. *Quaternary*
971 *International* 404, 44-56, <https://doi.org/10.1016/j.quaint.2015.09.032>.

972 Zhao, X., Dupont, L., Schefuß, E., Meadows, M.E., Hahn, A., Wefer, G., 2016b. Holocene
973 vegetation and climate variability in the winter and summer rainfall zones of South
974 Africa. *The Holocene* 26, 843-857, <https://doi.org/10.1177/0959683615622544>.