



HAL
open science

Extreme hydroclimate response gradients within the western Cape Floristic region of South Africa since the Last Glacial Maximum

Brian Chase, Arnoud Boom, Andrew Carr, Manuel Chevalier, Lynne J Quick, G. Anthony Verboom, Paula Reimer

► To cite this version:

Brian Chase, Arnoud Boom, Andrew Carr, Manuel Chevalier, Lynne J Quick, et al.. Extreme hydroclimate response gradients within the western Cape Floristic region of South Africa since the Last Glacial Maximum. *Quaternary Science Reviews*, 2019, 219, pp.297-307. 10.1016/j.quascirev.2019.07.006 . hal-02264496

HAL Id: hal-02264496

<https://hal.science/hal-02264496>

Submitted on 7 Oct 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 Extreme hydroclimate response gradients within the
2 western Cape Floristic region of South Africa since the Last
3 Glacial Maximum

4
5 The authors do not recommend the distribution of this version
6 of this article.

7 The article is freely available upon request.

8 To receive a copy, please send a request to Brian Chase at:
9 brian.chase@umontpellier.fr

10
11
12 Brian M. Chase^{*,a}, Arnoud Boom^b, Andrew S. Carr^b, Manuel Chevalier^c, Lynne J. Quick^d,
13 G. Anthony Verboom^e, Paula J. Reimer^f

14
15 ^a*Institut des Sciences de l'Evolution-Montpellier (ISEM), University of Montpellier, Centre National de la Recherche
16 Scientifique (CNRS), EPHE, IRD, Montpellier, France;*

17 ^b*School of Geography, Geology and the Environment, University of Leicester, Leicester, LE1 7RH, UK;*

18 ^c*Institute of Earth Surface Dynamics, Geopolis, University of Lausanne, Quartier UNIL-Mouline, Bâtiment Géopolis,
19 CH-1015 Lausanne, Switzerland;*

20 ^d*African Centre for Coastal Palaeoscience, Nelson Mandela University, 6031 Port Elizabeth, South Africa;*

21 ^e*Department of Biological Sciences, University of Cape Town, 7700 Rondebosch, South Africa;*

22 ^f*School of Natural and Built Environment, Queen's University Belfast, Belfast, BT7 1NN, Northern Ireland, UK;*

23
24 ***Correspondence and requests should be addressed to: Brian.Chase@umontpellier.fr, +33 (0)6 01 06 64 04**

26 **Abstract**

27 The Cape Floristic Region (CFR) is one of the world's major biodiversity hotspots, and much
28 work has gone into identifying the drivers of this diversity. Considered regionally in the context
29 of Quaternary climate change, climate stability is generally accepted as being one of the major
30 factors promoting the abundance of species now present in the CFR. However, little direct
31 evidence is available from the region, and responses to changes in global boundary conditions
32 have been difficult to assess. In this paper, we present new high-resolution stable isotope data
33 from Pakhuis Pass, in the species-rich western CFR, and contextualise our findings through
34 comparison with other records from the region. Combined, they indicate clear, coherent
35 changes in regional hydroclimate, which we relate to broader forcing mechanisms. However,
36 while these climate change events share similar timings (indicating shared macro-scale drivers),
37 the responses are distinct between sites, in some cases expressing opposing trends over very
38 short spatial gradients (<50 km). We describe the evolution of these trends, and propose that
39 while long-term (10^5 yr) general climatic stability may have fostered high diversity in the region
40 through low extinction rates, the strong, abrupt changes in hydroclimate gradients observed in
41 our records may have driven a form of allopatric speciation pump, promoting the diversification
42 of plant lineages through the periodic isolation and recombination of plant populations.

43 **Keywords**

44 Palaeoclimate, climate dynamics, South Africa, Cape Floristic Region, biodiversity, rock hyrax
45 middens, stable isotopes

46 **Highlights**

- 47 • New high resolution $\delta^{15}\text{N}$ data from rock hyrax middens from the western Cape Floristic
48 Region.
- 49 • Position of the southern westerlies apparent as a strong determinant of regional
50 hydroclimates.
- 51 • High amplitude, rapid changes in hydroclimate are revealed in the region.
- 52 • Opposing responses to shared climate change events establish highly variable climate
53 gradients.

54 **1 Introduction**

55 Southern African hydroclimate is primarily defined by the advection and precipitation of
56 moisture from tropical Atlantic and Indian Ocean sources during the austral summer (Figure 1).
57 In contrast, southwestern South Africa experiences a distinct, inverse rainfall regime. Seasonal
58 expansions of the circumpolar vortex and equatorward migration of the westerly storm track
59 bring increased precipitation during winter months, while displacements of the South Atlantic
60 Anticyclone during the summer intensify upwelling along the west coast, blocking the westward
61 propagation of easterly waves, generating strong summer drought in the region (Tyson, 1986;
62 Tyson and Preston-Whyte, 2000). During the Quaternary, southern Africa is thought to have
63 been sensitive to long-term changes in these tropical and temperate systems. Driven by
64 changes in global boundary conditions, tropical systems are invigorated during interglacial
65 periods and temperate systems exert increased influence during glacial periods (Chase et al.,
66 2015a; Chase et al., 2017; see Chase and Meadows, 2007; Cockcroft et al., 1988; Quick et al.,
67 2011; van Zinderen Bakker, 1976).

68 This dynamic, which is thought to have become dominant in the Plio-Pleistocene (5.0 –
69 2.6 Ma) when trade wind-controlled upwelling was established as a dominant factor in the
70 regional climate system (Diekmann et al., 2003), has created a Mediterranean climate zone in
71 the southwestern Cape of South Africa (Figure 2). This climatic evolution has been a key factor
72 in fostering the development of the vegetation of the Cape Floristic Region (CFR), which is
73 remarkable for its high level of endemism and its species richness (Cowling, 1992; Goldblatt,
74 1978).

75 It has been recognised, however, that species diversity within the CFR, is not
76 homogeneous, with the winter-rain dominated western CFR having more than twice the species
77 per area of the eastern CFR, which currently experiences an aseasonal rainfall regime (Figure 2)
78 (Cowling et al., 1992; Cowling and Lombard, 2002; Cowling et al., 1997). During the Quaternary,
79 the western CFR has putatively experienced a continuous dominance of temperate systems,
80 whereas the eastern CFR rainfall regimes may have oscillated between temperate and tropical
81 rainfall dominance (see Chase and Meadows, 2007) with much more significant consequences
82 on the distribution and nature of environmental niches (Cowling et al., 1999; Cowling et al.,
83 1992). With a reliable climate regime, and relatively muted cycles of Quaternary climate change
84 compared to the extratropical regions in the Northern Hemisphere (see Chase and Meadows,
85 2007; Dynesius and Jansson, 2000), it is believed that the CFR's great floral diversity –
86 particularly in the west – is largely attributable to relative climatic stability and resulting low
87 extinction rates (Cowling et al., 1992; Cowling and Lombard, 2002; Cowling et al., 2015; Cowling
88 et al., 1997; Linder, 2005; Verboom et al., 2014). These hypotheses, and the conclusion that the
89 western CFR represented a more durable climatic niche than the eastern CFR is supported by
90 analyses of phylogenetic diversity, which indicate that the western CFR experienced higher
91 levels of in situ radiation, while the eastern CFR indicates significant mixing of lineages from
92 different biomes (Forest et al., 2007; Verboom et al., 2014).

93 At broad spatio-temporal scales, it thus seems apparent that the development of, and
94 the dynamics within, the southwestern Cape's Mediterranean climate region were fundamental
95 determinants for the evolution of the CFR. At finer spatial and temporal scales, these
96 considerations become more complex. In the western CFR, it has been observed that species

97 richness is higher in the mountains than the lowlands, a situation related to topographic
98 variability and the resulting diversity of edaphic and climate spaces (Linder, 1991; Verboom et
99 al., 2015). Linder (1991) also found that species richness correlated most strongly with mean
100 annual precipitation, which might further suggest that climatic stability is a key determinant of
101 species diversity (as regions of currently high rainfall may be acting as interglacial refugia for
102 many CFR taxa (Chase and Meadows, 2007; Forest et al., 2007)). But how stable were climates
103 in these montane regions?

104 In this paper, we consider the climatic context of the high-diversity montane regions of
105 the western CFR in the light of new, high resolution palaeoclimatic data obtain from the region.
106 While neither spatially nor temporally comprehensive, it does enable the beginnings of a more
107 detailed analysis and understanding of the nature of climate change dynamics in the region.
108 While some studies have suggested long-term millennial-scale climate and vegetation stability
109 (Meadows et al., 2010; Meadows and Sugden, 1991), a growing body of data indicates
110 potentially more dynamic patterns of climate change, and further indicates that spatial climate
111 gradients may be much more complex than previously supposed (Chase et al., 2015a; Chase et
112 al., 2011). To address this, we present a new 19,300-year stable isotope composite record
113 derived from rock hyrax middens from Pakhuis Pass in the Cederberg Mountains. Considered
114 together with the records from other hyrax midden records from De Rif (Chase et al., 2015a;
115 Chase et al., 2011) and Katbakkies Pass (Chase et al., 2015b; Meadows et al., 2010), we are able
116 to assess the spatio-temporal dynamics of climate change along a modern climatic gradient in
117 the Cape Fold Belt Mountains of the western CFR – across the eastern slope of the Cederberg ,
118 and determine to what extent regional climates can be considered to be stable.

119 **1.1 Regional setting**

120 Pakhuis Pass is located in the northern Cederberg Mountains, the dominant range of the north-
121 south axis of the Cape Fold Mountains to the east and northeast of Cape Town (Figures 2, 3).
122 Extending for ~200 km parallel to the Atlantic Ocean (50-100 km to the west), this western limb
123 of the Cape Fold Belt is a significant divide between the relatively humid climates of the
124 southwestern Cape and the arid Karoo, which dominates much of South Africa's western
125 continental interior. The range also broadly marks the divide between southern Africa's two
126 major climate regimes: the winter rainfall zone (WRZ) to the west and the summer rainfall zone
127 (SRZ) to the northeast (cf. Chase and Meadows, 2007). The winter rainfall zone is defined by the
128 seasonal intensification and northward expansion of the westerlies and associated frontal
129 depressions that transport moisture to the region during the austral winter months. To the
130 east, and across most of South Africa, tropical easterly flow transports moisture from the Indian
131 Ocean during the austral summer. The Cederberg and adjacent ranges act as an orographic
132 divide between these climate zones, with the mountains creating a distinct rainshadow for
133 westerly derived rainfall (Figure 3; Tyson, 1986; Tyson and Preston-Whyte, 2000). The higher
134 elevations receive five times the precipitation of the lowlands to the east, but perhaps more
135 importantly, while the Cederberg Mountains receive more than 75% of their rainfall during the
136 winter, the lowlands to the east currently receive 50% or more of their precipitation during the
137 summer (Hijmans et al., 2005) (Figure 1).

138 Pakhuis Pass is located at ~485 m.a.s.l. on the eastern slopes of the Cederberg, in the
139 rainshadow of the Pakhuisberge massif (~1000 m.a.s.l.) (Figure 3). Mean annual rainfall at the
140 site is ~250-300 mm/yr, ~80% of which falls in the austral winter between April and September

141 (Hijmans et al., 2005). In comparison, the hyrax midden sites at De Rif (Chase et al., 2015a;
142 Chase et al., 2011; Quick et al., 2011) and Katbakkies Pass (Chase et al., 2015b; Meadows et al.,
143 2010) (Figure 2, 3) are both situated at ~1150 m.a.s.l., receive ~400 mm/yr and ~300 mm/yr of
144 mean annual rainfall respectively, and by virtue of their elevation and position relative to the
145 region's major topographic features they are more likely to receive precipitation during the
146 summer months through orographic amplification of local or larger synoptic-scale systems
147 (Tyson, 1986; Tyson and Preston-Whyte, 2000).

148 **2 Material and methods**

149 Middens for this study, PK08 and PK10-1 (Figure 4) were collected from the same ~400 m long,
150 15 m high cliff band (32.093°S, 19.065°E) as those described by Scott and Woodborne (2007a,
151 b) and were selected for their high hyraceum (crystallised urine) relative to faecal pellet
152 content. Apart from having greater structural integrity and less variable deposition rates,
153 hyraceum represents environmental conditions more clearly than samples containing faecal
154 pellets, which may potentially include a degree of dietary bias and often exhibit far more
155 discontinuous/irregular deposition (Chase et al., 2012). Sections of each midden were cut
156 perpendicular to the stratigraphy using an angle grinder and/or rotary impact hammer (Figure
157 4) and transported back to the laboratory for analysis. In addition to these newly collected
158 middens, we analysed one of the Pakhuis Pass middens (PK1173) considered in the papers of
159 Scott and Woodborne (2007a, b)

160 **2.1 Chronology**

161 Radiocarbon age determinations for the PK08 and PK10-1 middens (n=14) were processed at
162 the ¹⁴CHRONO Centre, Queen's University Belfast using accelerator mass spectrometry (AMS)
163 (Table 1; Figure 5). Samples were pre-treated with 2% HCl for one hour at room temperature to
164 remove carbonates and dried at 60°C. They were then weighed into quartz tubes with an excess
165 of CuO, sealed under vacuum and combusted to CO₂. The CO₂ was converted to graphite on an
166 iron catalyst using the zinc reduction method (Slota et al., 1987). The radiocarbon ages were
167 corrected for isotope fractionation using the AMS measured δ¹³C. These ages and those
168 obtained from PK1173 (Scott and Woodborne, 2007a) were calibrated using the SHCal13
169 calibration data (Hogg et al., 2013). The Clam 2.2 software package (Blaauw, 2010) was used to
170 generate all age-depth models (Figure 5). Clam was chosen over Bayesian techniques such as
171 Bacon (Blaauw and Christen, 2011) because strong changes in accumulation rate may occur in
172 hyrax middens (such as PK08 and PK10-1), and Clam – using linear models - is better suited to
173 such sequences.

174 **2.2 Stable nitrogen isotopes**

175 Stable nitrogen isotope analysis of midden hyraceum samples were performed at the
176 Department of Archaeology, University of Cape Town following Chase et al. (2010; 2009), with a
177 contiguous/overlapping samples obtained two series of offset 1 mm holes. The standard
178 deviation derived from replicate analyses of homogeneous material was better than 0.2 ‰.
179 Results are expressed relative to atmospheric nitrogen.

180 **3 Results**

181 **3.1 Chronology**

182 Radiocarbon analyses indicate that the Pakhuis Pass hyrax middens accumulated during the late
183 Pleistocene and Holocene, spanning the last ~19,300 years cal (calibrated) BP. The age-depth
184 models for the two middens suggest continuous deposition, although accumulation rates do
185 vary considerably (Table 1; Figure 5). Accumulation rates for the PK08 midden average ~28 μm
186 yr^{-1} , with a period of more rapid accumulation centred on 6000 cal BP (~132 $\mu\text{m yr}^{-1}$). Each 1
187 mm isotope sample from PK08 therefore integrates between ~8 and 105 years of hyraceum
188 accumulation (averaging 42 mm yr^{-1}). Accumulation rates for the PK10-1 midden increase with
189 age/depth, from ~2.6 $\mu\text{m yr}^{-1}$ in the uppermost 30 mm to ~106 $\mu\text{m yr}^{-1}$ in the bottom 13 mm.
190 Therein, each 1 mm isotope sample from PK10-1 integrates between ~380 years (upper section)
191 to ~10 years (lower section) of hyraceum accumulation. Because of this significant change in
192 accumulation rate, we show data from the extremely low resolution of the Holocene portion of
193 PK10-1, but do not consider it our analyses, favouring? the much more highly resolved record
194 from PK08. Accumulation of the PK1173 midden (Scott and Woodborne, 2007a) was more
195 regular, averaging ~50 $\mu\text{m yr}^{-1}$, with each isotope sample integrating ~20 years of accumulation.

196 **3.2 Stable nitrogen isotopes**

197 The $\delta^{15}\text{N}$ values from the PK08, PK10-1 and PK1173 middens vary from 3.6 to 8.6‰ (Figure 6).
198 Variations in midden $\delta^{15}\text{N}$ are interpreted to reflect changes in water availability (see more
199 extensive discussion in Chase et al., 2012). At the global scale, a relationship has been
200 recognised between aridity and foliar ^{15}N (e.g. Craine et al., 2009; Hartman and Danin, 2010),

201 and replication of this signal in plant and animal tissues and in faecal matter (e.g. Carr et al.,
202 2016; Hartman, 2011; Murphy and Bowman, 2006; Newsome et al., 2011) has been
203 demonstrated. This is thought to be generally a function of a more open nitrogen cycle in arid
204 regions. Fractionating pathways in the soil (nitrification, denitrification, etc.) mean that
205 nitrogen lost through transformation and the release of gaseous products is depleted in ^{15}N ,
206 and the remaining nitrogen is enriched. While in more humid regions N is cycled between live
207 and dead organic pools, in drier regions more N flows to mineral pools where it is subject to
208 gaseous loss (Amundson et al., 2003), and the $\delta^{15}\text{N}$ value of soils is thus higher with increasing
209 aridity (Austin and Vitousek, 1998; Handley et al., 1999; Murphy and Bowman, 2009). The
210 environmental processes relating to this recycling or loss of ^{15}N are not tied exclusively to
211 rainfall amount, but in climatic terms are more accurately considered to relate to water
212 availability (Murphy and Bowman, 2006). Studies of ^{15}N in hyrax middens from a wide range of
213 environments indicate consistently strong correlations between midden ^{15}N , local
214 vegetation/soil ^{15}N , as well as independent climate proxy records, supporting the conclusion
215 that environmental moisture availability is a major driver of midden ^{15}N records (Carr et al.,
216 2016; Chase et al., 2015a; Chase et al., 2013; Chase et al., 2017; Chase et al., 2015b; Chase et
217 al., 2010; Chase et al., 2009; Chase et al., 2011).

218 This general relationship may also be influenced to some extent by other (e.g.
219 microclimatic) factors, as is reflected in the variability observed in the relationship between
220 modern foliar ^{15}N and aridity estimates (e.g. Hartman and Danin, 2010; Murphy and Bowman,
221 2006; Peri et al., 2012). This influence can be observed in the offset between the PK08 and
222 PK1173 records and the record from PK10-1 (Figure 6). This is not uncommon when comparing

223 records from different middens, even when in relatively close proximity (<20 m) (Chase et al.,
224 2013). These differences are believed to be driven by micro-topographic variations influencing
225 water-availability in the primary feeding zones associated with each shelter (cf. Chase et al.,
226 2013; Chase et al., 2017). In the case of the Pakhuis Pass middens, PK10-1 was retrieved from a
227 narrow upper tier of the cliff complex, with the primary foraging range was likely to have been
228 dominated by plants able to establish in the exposed landscape and thin soils found on the rock
229 shelves above the cliff. PK08 and PK1173, in contrast, are located near the cliff base, and
230 surrounded by deeper soils and higher groundwater recharge potential, which supports a more
231 mesic, denser vegetation. The result is that while trends in $\delta^{15}\text{N}$ variability are similar between
232 the PK08, PK1173 and PK10-1 middens, the PK10-1 values are approximately 0.95‰ higher
233 (established by comparison of average values for the overlapping sections of midden
234 sequences). For combination and consideration of the records, we have applied a 0.95‰
235 correction factor to the PK10-1 data.

236 To create a single composite record, we selected the PK08 record over the much lower
237 resolution PK10-1 record for the mid- to late Holocene, as the latter is little informative in this
238 context, with greater temporal averaging attenuating the variability evident in the higher
239 resolution PK08 record. For the late Pleistocene, PK10-1 and PK1173 are of similar resolution
240 and indicate similar trends. To incorporate information from both middens, we combined and
241 smoothed the age-ranked data ensemble using Gaussian kernel-based interpolation (Rehfeld et
242 al., 2011). This technique has been shown to be the most appropriate to interpolate irregularly
243 sampled time series. We followed the recommendation of Rehfeld et al. (2011) and used the
244 average temporal resolution of the data from these sections (31.97 years) to define the width

245 of our Gaussian kernel. To maintain the true temporal resolution of our composite record, the
246 values were interpolated at the sample ages.

247 As a whole, the Pakhuis Pass $\delta^{15}\text{N}$ data indicate a general aridification at the site (change
248 towards higher $\delta^{15}\text{N}$ values) from the late Pleistocene to the Holocene (Figure 6). The most
249 humid periods recorded occur during the last glacial period, between 19,300 and 15,300 cal BP,
250 and from 6100-5500 cal BP, following the early to mid-Holocene transition. Maximum aridity is
251 reached during the early Holocene. The length and resolution of the records do not allow for
252 definitive comparisons, but variability during the Pleistocene portion of the record – even
253 considering its lower resolution - appears relatively muted compared to the strong, abrupt
254 changes apparent in the Holocene.

255 Using change point analysis (Killick et al., 2012; Trauth et al., 2018), major transitions in
256 the mean climate state (not accounting for changes in variability) in the record (where the root-
257 mean-square level of the signal changes most significantly) were identified. Most notably, the
258 period following the termination of early Holocene aridity at ~6800 cal BP is marked by a series
259 of abrupt changes reflecting a rapid increase in water availability between ~6800 and 6140 cal
260 BP. This period of relatively humid conditions ends equally abruptly, with distinctly drier
261 conditions persisting from 5520 - 4480 cal BP. A subsequent sharp increase in water availability
262 is followed by a gradual aridification between 4480 and 2830 cal BP, and apparently more
263 stable conditions during the late Holocene. It is worth noting that the amplitude of change
264 registered across these transitions (as much as 4.5‰) is similar to the amplitude of change
265 between the Last Glacial Maximum and Holocene (5‰). Using the data derived from modern

266 hyrax faecal pellets presented by Carr et al. (2016), this may speculatively be translated to a
267 ~70% increase in water availability (Aridity Index from 0.25 to 0.42) for the period between
268 ~6800 and 6100 cal BP (Figure 6). Unfortunately, the midden records obtained do not provide
269 detailed information regarding modern/sub-modern conditions, and a full contextualisation of
270 these results in comparison with modern climates and recent change is not yet possible.

271 **4 Discussion**

272 **4.1 Glacial-interglacial scale variability**

273 Considering the combined influences of lower Pleistocene temperatures (Chevalier and Chase,
274 2016; Lim et al., 2016; Stute and Talma, 1998; Talma and Vogel, 1992), and the position of
275 Pakhuis Pass in the winter rainfall zone, which is considered to have received increased
276 precipitation during glacial periods (Chase et al., 2017; Chase and Meadows, 2007; Cockcroft et
277 al., 1987; van Zinderen Bakker, 1976), it is not surprising that the late Pleistocene is
278 characterised by more humid conditions (Figure 7). What is most remarkable about the Pakhuis
279 Pass $\delta^{15}\text{N}$ record is that it indicates dramatically different patterns of change than those
280 recorded at the De Rif hyrax midden site, located only 42 km to the south (Figure 2,3; Chase et
281 al. 2011, 2015). This implies past climate change dynamics characterised by marked levels of
282 spatio-temporal heterogeneity. Previously, inter-regional differences have been indicated by
283 $\delta^{15}\text{N}$ records from Seweweekspoort (Figure 2; 230 km east-southeast of De Rif). In isolation, the
284 differences between the De Rif and Seweweekspoort might otherwise have been explained by
285 the distinct natures of eastern and western CFR climate histories (Chase and Meadows, 2007;
286 Cowling et al., 1992). The new data from Pakhuis Pass imply a more complex dynamic.

287 Interpretations of the Seweweekspoort and De Rif records, which extend into the Last
288 Glacial Maximum (LGM; 19-26.5 ka (Clark et al., 2009)) have highlighted the influence of
289 different elements of the regional climate system as they were impacted by changing global
290 boundary conditions. At glacial-interglacial timescales, the $\delta^{15}\text{N}$ record from Seweweekspoort
291 (Chase et al., 2017) has been identified as primarily reflecting changes in the climate system
292 related to global temperature and Antarctic sea-ice, which has been hypothesised as being a
293 significant control on the position of the southern westerlies storm track (Chase and Meadows,
294 2007; Cockcroft et al., 1987; van Zinderen Bakker, 1976). In contrast, at De Rif, despite being
295 closer to the core of the WRZ, where temperate systems define the modern regional rainfall
296 regime, the primary control on hydrologic balance at millennial and multi-millennial timescales
297 appears to be variations in the length and intensity of the summer drought season, potentially
298 modulated by variations in the intensity of the South Atlantic Anticyclone, which blocks the
299 incursion of tropical air masses and limits convection (Chase et al., 2015a). In the higher
300 elevations of the Cederberg mountains, while winter rainfall is consistent and abundant,
301 changes in summer rainfall may have had a more significant influence on driving drought-stress
302 at the site. Including the new Pakhuis Pass $\delta^{15}\text{N}$ record in this regional consideration, it seems
303 likely (based on similarities in first-order trends with SWP, as well as EPICA Dronning Maud Land
304 ice core sea-salt sodium flux record, considered as a general proxy for sea-ice extent (Fischer et
305 al., 2007)) that at glacial-interglacial timescales conditions at Pakhuis Pass is predominantly
306 impacted by changes in temperate system influence, with summer rainfall playing a relatively
307 limited role in defining water availability.

308 4.2 The Holocene

309 Focussing on the Holocene, more, and more precise data can be brought to bear on the
310 question of CFR climate dynamics. While data coverage remains far from comprehensive, high
311 resolution stable isotope data from rock hyrax middens have provided important clues as to
312 some of the drivers and spatial dynamics that have defined climate change in the region during
313 the Holocene (Figure 8). Building from the basis of the conceptual models developed by van
314 Zinderen Bakker (1976) and Cockcroft et al. (1987), which indicate that periods of global cooling
315 (warming) will generally result in wetter (drier) conditions in the WRZ (SRZ), and that a coeval
316 inverse relationship in terms of precipitation amount exists between the two regions, more
317 nuanced scenarios regarding observed variability are being proposed.

318 To constrain the relationship between CFR climate dynamics and the underlying drivers
319 of the observed variability, we have considered the diatom-based Atlantic sector sea-ice extent
320 and Southern Ocean summer sea-surface temperature (SSST) reconstructions of Nielsen et al.
321 (2004) from marine core TN057-17. Similarities with these records can be observed at sites
322 across the CFR, but it appears that the relationship between humidity and mid-latitude SSSTs
323 changes from positive to negative moving from the eastern to western CFR. At the coastal
324 eastern CFR site of Eilandvlei (Quick et al., 2018), for example, higher percentages of
325 afrotemperate forest pollen (considered to indicate increased humidity and reduced drought
326 stress) correlate well with higher SSSTs at TN057-17 (Figure 8). In contrast, higher humidity at
327 Pakhuis and Katbakkies passes are more clearly linked to lower SSSTs. Climatically, this most
328 likely indicates that increased westerly influence results in more humid conditions in the lee of

329 the Cederberg mountains, perhaps related to a greater frequency of more powerful frontal
330 systems.

331 Considering the relationship between the Pakhuis and Katbakkies pass sites, the impact
332 of changes in westerly influence is variable even between these two sites, despite their
333 proximity and their shared position in the lee of the Cederberg. Katbakkies Pass $\delta^{15}\text{N}$ record
334 exhibits changes in both the timing and amplitude that are similar to changes in TN057-17
335 SSSTs, perhaps indicating that variations in humidity are more tightly coupled to temperate
336 frontal systems than at Pakhuis Pass, where the timing and direction of the anomalies is shared,
337 but the local response is less consistent (Figure 8). As has been indicated (Chase et al., 2017),
338 increased frontal activity during the Holocene is not necessarily inconsistent with the increases
339 in summer rain that have been previously suggested to drive moisture availability at Katbakkies
340 Pass (Chase et al., 2015b), but it is clear that further work is required to adequately understand
341 how temperate and tropical systems interact to create precipitation events in the region on the
342 timescales considered here.

343 Underscoring the regional heterogeneity and the variable influence of the region's
344 moisture bearing systems, the Holocene record from De Rif once again is markedly different
345 from the Pakhuis and Katbakkies pass sites (Figure 8). Whereas the Pakhuis and Katbakkies Pass
346 records exhibit a generally negative relationship between humidity and TN057-17 SSSTs, at De
347 Rif the relationship is generally positive, with more humid conditions occurring during periods
348 of relatively elevated SSSTs. In the early Holocene, while sea ice presence is low in the Atlantic
349 sector of the Southern Ocean, conditions at De Rif are at their most humid for the last 19,400

350 years. With cooling SSSTs and increased sea ice presence after 7000 cal BP, conditions become
351 significantly drier. This extreme change during the early to mid-Holocene transition exemplifies
352 the apparently sharply contrasting trends across the region, with the records from both Pakhuis
353 and Katbakkies pass showing a strong increase in humidity evident from ~7000 – 6000 cal BP.
354 While more muted, this coeval inverse relationship between the Pakhuis and Katbakkies Pass
355 passes? sites and the De Rif persists throughout the Holocene, indicating that conditions at all
356 of the sites are controlled by a shared dynamic, but that opposing factors determine conditions
357 in the mountains (De Rif) and the rainshadow (Pakhuis and Katbakkies passes).

358 Of particular significance is how the opposing responses affect climatic gradients across
359 the region. During the early Holocene, based on the $\delta^{15}\text{N}$ data, a very strong hydroclimatic
360 gradient existed along the eastern slope of the Cederberg Mountains (Figure 9). Following the
361 early to mid-Holocene transition, this gradient became much weaker, with more similar
362 hydroclimatic conditions existing between the western CFR sites considered here. While only
363 the records from De Rif and Pakhuis Pass extend to the Last Glacial Maximum, indications are
364 that these gradients were weakened even further during the late Pleistocene, with similar $\delta^{15}\text{N}$
365 values at both sites suggesting nearly equivalent hydroclimatic conditions.

366 We hypothesise that these changes in environmental gradients may have had a
367 significant influence on the diversity and distinction of environmental niches in the region, and
368 that changes in these gradients may have acted as locks for gene flow, serving to alternatively
369 isolate or enable the migration and mixing of plant species across the region. Considering the
370 observation that species richness in the western CFR is higher in montane regions, the data

371 presented here provide palaeoclimatic evidence that highly variable spatial environmental
372 gradients may have acted as a kind of allopatric speciation pump (e.g. Goldblatt and Manning,
373 2002; Haffer, 1969; Linder, 1985; Linder, 2003; Verboom et al., 2015), with the repeated
374 isolation and mixing of promoting the exceptionally high species diversity of the CFR.

375 Further work will be required to establish where and to what extent variability on the
376 scale discussed in this paper has been biologically significant. Has the degree or rate of change
377 exceeded the tolerance of specific plant species or their ability to migrate? Can the spatial
378 configuration of climate response anomalies be reliably linked to spatial patterns of species
379 richness? Or, are the changes observed in the records discussed largely insignificant, and play
380 no consequential role in determining species richness. Studies of fossil pollen records from the
381 region provide a mixed response, with some indicating only minor changes in vegetation
382 composition during the late Pleistocene and Holocene (Meadows et al., 2010; Meadows and
383 Sugden, 1991), while other indicate substantial changes in vegetation have occurred (Scott and
384 Woodborne, 2007a; Valsecchi et al., 2013). To adequately evaluate and compare these findings,
385 more sites from transects across the region will need to be studied using a consistent
386 methodology that employs a range of proxies capable of differentiating climate and vegetation
387 change, and assessing spatial patterns of genetic diversity.

388 **5 Conclusions**

- 389 • We present a new, high resolution $\delta^{15}\text{N}$ record from Pakhuis Pass in the Cederberg
390 Mountains of the western Cape Floristic Region.

- 391 • Like recently published records from the region (Chase et al., 2015a; Chase et al.,
392 2015b), the data from Pakhuis Pass indicate substantial, rapid changes in hydroclimatic
393 conditions, contrasting with earlier suggestions that the Cederberg experienced
394 relatively little environmental change during since the LGM (Meadows et al., 2010;
395 Meadows and Sugden, 1991).
- 396 • The record from Pakhuis Pass indicates similarities with patterns of change observed in
397 comparable records from Katbakkies Pass ((Chase et al., 2015b), also in the rainshadow
398 of the Cederberg) but contrasts sharply with conditions at De Rif (Chase et al., 2015a),
399 where a coeval inverse pattern of variability is observed. Commonalities in the *timing* of
400 change suggest a shared driver of regional climate dynamics, but distinct local
401 responses, perhaps as a function of orographic influences.
- 402 • The opposing regional responses indicate significant changes in environmental
403 gradients across the western CFR.
- 404 • While hydroclimatic conditions at Pakhuis Pass and De Rif may have been similar
405 immediately after the LGM, subsequent responses to changes in global boundary
406 conditions during deglaciation resulted in the establishment of a steep environmental
407 gradient between the sites.
- 408 • We hypothesise that changes in the slope of this gradient likely reflect similar patterns
409 across the region, and that these changes may have driven an allopatric speciation
410 pump, contributing to the elevated species diversity observed in the montane regions of
411 the western CFR.

- 412 • The spatial heterogeneity of hydroclimatic conditions suggested by the data included in
413 this study indicates the need for more sites and comparable data from across the CFR in
414 order to resolve the complexity of response to long-term climate change.

415 **6 Acknowledgements**

416 The research leading to these results has received funding from the European Research Council
417 under the European Union's Seventh Framework Programme (FP7/2007-2013), ERC Starting
418 Grant “HYRAX”, grant agreement no. 258657. We are very grateful to Louis Scott for providing a
419 portion of the PK1173 midden for analysis.

420 **7 References**

- 421 Amundson, R., Austin, A.T., Schuur, E.A.G., Yoo, K., Matzek, V., Kendall, C., Uebersax, A.,
422 Brenner, D., Baisden, W.T., 2003. Global patterns of the isotopic composition of soil and plant
423 nitrogen. *Global Biogeochemical Cycles* 17.
- 424 Austin, A.T., Vitousek, P.M., 1998. Nutrient dynamics on a precipitation gradient in Hawai'i.
425 *Oecologia* 113, 519-529.
- 426 Blaauw, M., 2010. Methods and code for 'classical' age-modelling of radiocarbon sequences.
427 *Quaternary Geochronology* 5, 512-518.
- 428 Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an
429 autoregressive gamma process. *Bayesian Analysis* 6, 457-474.
- 430 Carr, A.S., Chase, B.M., Boom, A., Medina-Sanchez, J., 2016. Stable isotope analyses of rock
431 hyrax faecal pellets, hyraceum and associated vegetation in southern Africa: Implications for
432 dietary ecology and palaeoenvironmental reconstructions. *Journal of Arid Environments* 134, 33-
433 48.
- 434 Chase, B.M., Boom, A., Carr, A.S., Carré, M., Chevalier, M., Meadows, M.E., Pedro, J.B.,
435 Stager, J.C., Reimer, P.J., 2015a. Evolving southwest African response to abrupt deglacial North
436 Atlantic climate change events. *Quaternary Science Reviews* 121, 132-136.
- 437 Chase, B.M., Boom, A., Carr, A.S., Meadows, M.E., Reimer, P.J., 2013. Holocene climate
438 change in southernmost South Africa: rock hyrax middens record shifts in the southern
439 westerlies. *Quaternary Science Reviews* 82, 199-205.
- 440 Chase, B.M., Chevalier, M., Boom, A., Carr, A.S., 2017. The dynamic relationship between
441 temperate and tropical circulation systems across South Africa since the last glacial maximum.
442 *Quaternary Science Reviews* 174, 54-62.

443 Chase, B.M., Lim, S., Chevalier, M., Boom, A., Carr, A.S., Meadows, M.E., Reimer, P.J., 2015b.
444 Influence of tropical easterlies in southern Africa's winter rainfall zone during the Holocene.
445 Quaternary Science Reviews 107, 138-148.

446 Chase, B.M., Meadows, M.E., 2007. Late Quaternary dynamics of southern Africa's winter
447 rainfall zone. Earth-Science Reviews 84, 103-138.

448 Chase, B.M., Meadows, M.E., Carr, A.S., Reimer, P.J., 2010. Evidence for progressive Holocene
449 aridification in southern Africa recorded in Namibian hyrax middens: implications for African
450 Monsoon dynamics and the "African Humid Period". Quaternary Research 74, 36-45.

451 Chase, B.M., Meadows, M.E., Scott, L., Thomas, D.S.G., Marais, E., Sealy, J., Reimer, P.J.,
452 2009. A record of rapid Holocene climate change preserved in hyrax middens from southwestern
453 Africa. Geology 37, 703-706.

454 Chase, B.M., Quick, L.J., Meadows, M.E., Scott, L., Thomas, D.S.G., Reimer, P.J., 2011. Late
455 glacial interhemispheric climate dynamics revealed in South African hyrax middens. Geology
456 39, 19-22.

457 Chase, B.M., Scott, L., Meadows, M.E., Gil-Romera, G., Boom, A., Carr, A.S., Reimer, P.J.,
458 Truc, L., Valsecchi, V., Quick, L.J., 2012. Rock hyrax middens: a palaeoenvironmental archive
459 for southern African drylands. Quaternary Science Reviews 56, 107-125.

460 Chevalier, M., 2019. Enabling possibilities to quantify past climate from fossil assemblages at a
461 global scale. Global and Planetary Change 175, 27-35.

462 Chevalier, M., Chase, B.M., 2016. Determining the drivers of long-term aridity variability: a
463 southern African case study. Journal of Quaternary Science 31, 143-151.

464 Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X.,
465 Hostetler, S.W., McCabe, A.M., 2009. The Last Glacial Maximum. Science 325, 710-714.

466 Cockcroft, M.J., Wilkinson, M.J., Tyson, P.D., 1987. The application of a present-day climatic
467 model to the late Quaternary in southern Africa. Climatic Change 10, 161-181.

468 Cockcroft, M.J., Wilkinson, M.J., Tyson, P.D., 1988. A palaeoclimatic model for the late
469 Quaternary in southern Africa. Palaeoecology of Africa 19, 279-282.

470 Cowling, R.M., 1992. The Ecology of Fynbos: Nutrients, Fire, and Diversity. Oxford University
471 Press, Cape Town.

472 Cowling, R.M., Cartwright, C.R., Parkington, J.E., Allsopp, J.C., 1999. Fossil wood charcoal
473 assemblages from Elands Bay Cave, South Africa: implications for Late Quaternary vegetation
474 and climates in the winter-rainfall fynbos biome. Journal of Biogeography 26, 367-378.

475 Cowling, R.M., Holmes, P.M., Rebelo, A.G., 1992. Plant diversity and endemism, in: Cowling,
476 R.M. (Ed.), Ecology of fynbos. Nutrients, Fire and Diversity. Oxford University Press, Cape
477 Town, pp. 62–112.

478 Cowling, R.M., Lombard, A.T., 2002. Heterogeneity, speciation/extinction history and climate:
479 explaining regional plant diversity patterns in the Cape Floristic Region. Diversity and
480 Distributions 8, 163-179.

481 Cowling, R.M., Potts, A.J., Bradshaw, P.L., Colville, J., Arianoutsou, M., Ferrier, S., Forest, F.,
482 Fyllas, N.M., Hopper, S.D., Ojeda, F., Procheş, Ş., Smith, R.J., Rundel, P.W., Vassilakis, E.,
483 Zutta, B.R., 2015. Variation in plant diversity in mediterranean-climate ecosystems: the role of
484 climatic and topographical stability. Journal of Biogeography 42, 552-564.

485 Cowling, R.M., Richardson, D.M., Schulze, R.J., Hoffman, M.T., Midgley, J.J., Hilton-Taylor,
486 C., 1997. Species diversity at the regional scale, in: Cowling, R.M., Richardson, D.M., Pierce,
487 S.M. (Eds.), Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp. 447–
488 473.

489 Craine, J.M., Elmore, A.J., Aidar, M.P.M., Bustamante, M., Dawson, T.E., Hobbie, E.A.,
490 Kahmen, A., Mack, M.C., McLauchlan, K.K., Michelsen, A., Nardoto, G.B., Pardo, L.H.,
491 Peñuelas, J., Reich, P.B., Schuur, E.A.G., Stock, W.D., Templer, P.H., Virginia, R.A., Welker,
492 J.M., Wright, I.J., 2009. Global patterns of foliar nitrogen isotopes and their relationships with
493 climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New*
494 *Phytologist* 183, 980-992.

495 Diekmann, B., Falker, M., Kuhn, G., 2003. Environmental history of the south-eastern South
496 Atlantic since the Middle Miocene: evidence from the sedimentological records of ODP Sites
497 1088 and 1092. *Sedimentology* 50, 511-529.

498 Dynesius, M., Jansson, R., 2000. Evolutionary consequences of changes in species' geographical
499 distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy*
500 *of Sciences* 97, 9115-9120.

501 Fischer, H., Fundel, F., Ruth, U., Twarloh, B., Wegner, A., Udisti, R., Becagli, S., Castellano, E.,
502 Morganti, A., Severi, M., Wolff, E., Littot, G., Röthlisberger, R., Mulvaney, R., Hutterli, M.A.,
503 Kaufmann, P., Federer, U., Lambert, F., Bigler, M., Hansson, M., Jonsell, U., de Angelis, M.,
504 Boutron, C., Siggaard-Andersen, M.-L., Steffensen, J.P., Barbante, C., Gaspari, V., Gabrielli, P.,
505 Wagenbach, D., 2007. Reconstruction of millennial changes in dust emission, transport and
506 regional sea ice coverage using the deep EPICA ice cores from the Atlantic and Indian Ocean
507 sector of Antarctica. *Earth and Planetary Science Letters* 260, 340-354.

508 Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A.,
509 Manning, J.C., Procheş, Ş., van der Bank, M., Reeves, G., Hedderson, T.A.J., Savolainen, V.,
510 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445, 757.

511 GBIF.org, 2018a. Anthocerotopsida occurrence data downloaded on September 13th. GBIF.org.
512 GBIF.org, 2018b. Cycadopsidae occurrence data downloaded on March 30th. GBIF.org.
513 GBIF.org, 2018c. Ginkgoopsidae occurrence data downloaded on March 30th. GBIF.org.
514 GBIF.org, 2018d. Gnetopsidae occurrence data downloaded on March 30th. GBIF.org.
515 GBIF.org, 2018e. Liliopsida occurrence data downloaded on September 13th. GBIF.org.
516 GBIF.org, 2018f. Lycopodiopsida occurrence data downloaded on September 13th. GBIF.org.
517 GBIF.org, 2018g. Magnoliopsida occurrence data downloaded on March 30th. GBIF.org.
518 GBIF.org, 2018h. Pinopsidae occurrence data downloaded on March 30th. GBIF.org.
519 GBIF.org, 2018i. Polypodiopsida occurrence data downloaded on September 13th. GBIF.org.

520 Goldblatt, P., 1978. An analysis of the flora of southern Africa: its characteristics, relationships,
521 and origins. *Annals of the Missouri Botanical Garden* 65, 369-436.

522 Goldblatt, P., Manning, J.C., 2002. Plant diversity of the Cape Region of southern Africa. *Annals*
523 *of the Missouri Botanical Garden* 89, 281-302.

524 Haffer, J., 1969. Speciation in Amazonian Forest Birds. *Science* 165, 131-137.

525 Handley, L.L., Austin, A.T., Stewart, G.R., Robinson, D., Scrimgeour, C.M., Raven, J.A.,
526 Heaton, T.H.E., Schmidt, S., 1999. The ^{15}N natural abundance ($\delta^{15}\text{N}$) of ecosystem samples
527 reflects measures of water availability. *Functional Plant Biology* 26, 185-199.

528 Hartman, G., 2011. Are elevated $\delta^{15}\text{N}$ values in herbivores in hot and arid environments caused
529 by diet or animal physiology? *Functional Ecology* 25, 122-131.

530 Hartman, G., Danin, A., 2010. Isotopic values of plants in relation to water availability in the
531 Eastern Mediterranean region. *Oecologia* 162, 837-852.

532 Hijmans, R., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution
533 interpolated climate surfaces for global land areas. *International Journal of Climatology* 25,
534 1965-1978.

535 Hogg, A.G., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Heaton, T.J.,
 536 Palmer, J.G., Reimer, P.J., Reimer, R.W., Turney, C.S.M., Zimmerman, S.R.H., 2013. SHCal13
 537 Southern Hemisphere Calibration, 0–50,000 Years cal BP. *Radiocarbon* 55, 1889-1903.
 538 Killick, R., Fearnhead, P., Eckley, I.A., 2012. Optimal Detection of Changepoints With a Linear
 539 Computational Cost. *Journal of the American Statistical Association* 107, 1590-1598.
 540 Lim, S., Chase, B.M., Chevalier, M., Reimer, P.J., 2016. 50,000 years of vegetation and climate
 541 change in the southern Namib Desert, Pella, South Africa. *Palaeogeography, Palaeoclimatology,*
 542 *Palaeoecology* 451, 197-209.
 543 Linder, H.P., 1985. Gene flow, speciation, and species diversity patterns in a species-rich area:
 544 the Cape Flora. *Species and speciation* 4, 53-57.
 545 Linder, H.P., 1991. Environmental correlates of patterns of species richness in the south-western
 546 Cape Province of South Africa. *Journal of Biogeography* 18, 509-518.
 547 Linder, H.P., 2003. The radiation of the Cape flora, southern Africa. *Biological Reviews of the*
 548 *Cambridge Philosophical Society* 78, 597-638.
 549 Linder, H.P., 2005. Evolution of diversity: the Cape flora. *Trends in Plant Science* 10, 536-541.
 550 Meadows, M.E., Chase, B.M., Seliane, M., 2010. Holocene palaeoenvironments of the
 551 Cederberg and Swartruggens mountains, Western Cape, South Africa: Pollen and stable isotope
 552 evidence from hyrax dung middens. *Journal of Arid Environments* 74, 786-793.
 553 Meadows, M.E., Sugden, J.M., 1991. A vegetation history of the last 14,000 years on the
 554 Cederberg, southwestern Cape Province. *South African Journal of Science* 87, 34-43.
 555 Mucina, L., Rutherford, M.C., 2006. The vegetation of South Africa, Lesotho and Swaziland,
 556 *Strelitzia*. South African National Biodiversity Institute, Pretoria.
 557 Murphy, B.P., Bowman, D.M.J.S., 2006. Kangaroo metabolism does not cause the relationship
 558 between bone collagen $\delta^{15}\text{N}$ and water availability. *Functional Ecology* 20, 1062-1069.
 559 Murphy, B.P., Bowman, D.M.J.S., 2009. The carbon and nitrogen isotope composition of
 560 Australian grasses in relation to climate. *Functional Ecology* 23, 1040-1049.
 561 Newsome, S.D., Miller, G.H., Magee, J.W., Fogel, M.L., 2011. Quaternary record of aridity and
 562 mean annual precipitation based on $\delta^{15}\text{N}$ in ratite and dromornithid eggshells from Lake Eyre,
 563 Australia. *Oecologia* 167, 1151-1162.
 564 Nielsen, S.H.H., Koç, N., Crosta, X., 2004. Holocene climate in the Atlantic sector of the
 565 Southern Ocean: Controlled by insolation or oceanic circulation? *Geology* 32, 317-320.
 566 Peri, P.L., Ladd, B., Pepper, D.A., Bonser, S.P., Laffan, S.W., Amelung, W., 2012. Carbon
 567 ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope composition in plant and soil in Southern Patagonia's
 568 native forests. *Global Change Biology* 18, 311-321.
 569 Quick, L.J., Chase, B.M., Meadows, M.E., Scott, L., Reimer, P.J., 2011. A 19.5 kyr vegetation
 570 history from the central Cederberg Mountains, South Africa: Palynological evidence from rock
 571 hyrax middens. *Palaeogeography, Palaeoclimatology, Palaeoecology* 309, 253-270.
 572 Quick, L.J., Chase, B.M., Wüdsch, M., Kirsten, K.L., Chevalier, M., Mäusbacher, R.,
 573 Meadows, M.E., Haberzettl, T., 2018. A high-resolution record of Holocene climate and
 574 vegetation dynamics from the southern Cape coast of South Africa: pollen and microcharcoal
 575 evidence from Eilandvlei. *Journal of Quaternary Science* 33, 487-500.
 576 Rehfeld, K., Marwan, N., Heitzig, J., Kurths, J., 2011. Comparison of correlation analysis
 577 techniques for irregularly sampled time series. *Nonlin. Processes Geophys.* 18, 389-404.
 578 Roberts, D.L., Neumann, F.H., Cawthra, H.C., Carr, A.S., Scott, L., Durugbo, E.U., Humphries,
 579 M.S., Cowling, R.M., Bamford, M.K., Musekiwa, C., MacHutchon, M., 2017.

580 Palaeoenvironments during a terminal Oligocene or early Miocene transgression in a fluvial
581 system at the southwestern tip of Africa. *Global and Planetary Change* 150, 1-23.

582 Scott, L., Woodborne, S., 2007a. Pollen analysis and dating of Late Quaternary faecal deposits
583 (hyraceum) in the Cederberg, Western Cape, South Africa. *Review of Palaeobotany and*
584 *Palynology* 144, 123-134.

585 Scott, L., Woodborne, S., 2007b. Vegetation history inferred from pollen in Late Quaternary
586 faecal deposits (hyraceum) in the Cape winter-rain region and its bearing on past climates in
587 South Africa. *Quaternary Science Reviews* 26, 941-953.

588 Slota, P.J., Jull, A.J.T., Linick, T.W., Toolin, L.J., 1987. Preparation of small samples for ^{14}C
589 accelerator targets by catalytic reduction of CO. *Radiocarbon* 29, 303-306.

590 Stute, M., Talma, A.S., 1998. Glacial temperatures and moisture transport regimes reconstructed
591 from noble gas and $\delta^{18}\text{O}$, Stampriet aquifer, Namibia, *Isotope Techniques in the Study of Past*
592 *and Current Environmental Changes in the Hydrosphere and the Atmosphere*. IAEA Vienna
593 Symposium 1997, Vienna, Austria, pp. 307-318.

594 Talma, A.S., Vogel, J.C., 1992. Late Quaternary paleotemperatures derived from a speleothem
595 from Cango Caves, Cape Province, South Africa. *Quaternary Research* 37, 203-213.

596 Trabucco, A., Zomer, R.J., 2009. Global Aridity Index (Global-Aridity) and Global Potential
597 Evapo-Transpiration (Global-PET) Geospatial Database. , in: Information, C.C.f.S. (Ed.).
598 CGIAR-CSI GeoPortal, <http://www.csi.cgiar.org>.

599 Trauth, M.H., Foerster, V., Junginger, A., Asrat, A., Lamb, H.F., Schaebitz, F., 2018. Abrupt or
600 gradual? Change point analysis of the late Pleistocene–Holocene climate record from Chew
601 Bahir, southern Ethiopia. *Quaternary Research*, 1-10.

602 Tyson, P.D., 1986. *Climatic Change and Variability in Southern Africa*. Oxford University Press,
603 Cape Town.

604 Tyson, P.D., Preston-Whyte, R.A., 2000. *The Weather and Climate of Southern Africa*. Oxford
605 University Press, Cape Town.

606 UNEP, 1997. *World atlas of desertification*, 2nd ed. United Nations Environment Programme,
607 London.

608 Valsecchi, V., Chase, B.M., Slingsby, J.A., Carr, A.S., Quick, L.J., Meadows, M.E., Cheddadi,
609 R., Reimer, P.J., 2013. A high resolution 15,600-year pollen and microcharcoal record from the
610 Cederberg Mountains, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 387,
611 6-16.

612 van Zinderen Bakker, E.M., 1976. The evolution of late Quaternary paleoclimates of Southern
613 Africa. *Palaeoecology of Africa* 9, 160-202.

614 Verboom, G.A., Linder, H.P., Forest, F., Hoffman, V., Bergh, N.G., Cowling, R.M., 2014.
615 Cenozoic assembly of the greater Cape flora, in: Allsopp, N., Colville, J.F., Verboom, G.A.
616 (Eds.), *Fynbos: Ecology, Evolution and Conservation of a Megadiverse Region*. Oxford
617 University Press, Oxford, pp. 93-118.

618 Verboom, G.A., Nicola, G.B., Sarah, A.H., Vera, H., Matthew, N.B., 2015. Topography as a
619 driver of diversification in the Cape Floristic Region of South Africa. *The New Phytologist* 207,
620 368-376.

621 Yamazaki, D., Ikeshima, D., Tawatari, R., Yamaguchi, T., O'Loughlin, F., Neal, J.C., Sampson,
622 C.C., Kanae, S., Bates, P.D., 2017. A high-accuracy map of global terrain elevations.
623 *Geophysical Research Letters* 44, 5844-5853.

624

625 **Table captions**

626 Table 1: Radiocarbon ages and calibration information for the PK08, PK10-1 and PK1173 (Scott
627 and Woodborne, 2007a, b) rock hyrax middens.

628 **Figure captions**

629 **Figure 1:** Map of southern Africa showing seasonality of rainfall and climatic gradients dictated
630 by the zones of summer/tropical (red) and winter/temperate (blue) rainfall dominance. Major
631 atmospheric (white arrows) and oceanic (blue arrows) circulation systems are indicated.

632 **Figure 2:** Map of southernmost Africa showing **A)** showing seasonality of rainfall and climatic
633 gradients defined in terms of percentage of winter rainfall, **B)** the extent of the vegetation
634 types comprising the Cape Floristic Region (fynbos, renosterveld and Albany Thicket (data from
635 Mucina and Rutherford, 2006)), **C)** a map of mean Aridity Index values for the region (Trabucco
636 and Zomer, 2009), and **D)** a map of species richness using data derived from the GBIF database
637 (Chevalier, 2019; 2018; GBIF.org, 2018, b, c, d, e, f, g, h, i); number of species per quarter-
638 degree grid cell were interpolated to create the contour map. Classification of aridity values
639 follows that of the United Nations Environment Programme (1997). Sites considered in this
640 study are indicated: Pakhuis Pass (PK: this study; Scott and Woodborne, 2007a; Scott and
641 Woodborne, 2007b), De Rif (DR: Chase et al., 2015a; Chase et al., 2011; Quick et al., 2011),
642 Katbakkies Pass (KB: Chase et al., 2015b; Meadows et al., 2010), Seweweekspoort (SWP: Chase
643 et al., 2015a; Chase et al., 2013; Chase et al., 2017) and Eilandvlei (Quick et al., 2018).

644 **Figure 3:** Map of the N-S axis of the Cape Fold Mountains in the southwestern Cape, including
645 the Cederberg Mountains and adjacent ranges. Topographic variability (MERIT digital elevation
646 model; Yamazaki et al., 2017) is overlain by a map of mean Aridity Index values (Trabucco and
647 Zomer, 2009) for the region, as in Figure 1. The dominant vector of temperate moisture-bearing
648 systems related to the westerly storm track is shown, as are the sites considered in this study:
649 Pakhuis Pass (this study; Scott and Woodborne, 2007a; Scott and Woodborne, 2007b), De Rif
650 (Chase et al., 2015a; Chase et al., 2011; Quick et al., 2011), Katbakkies Pass (Chase et al., 2015b;
651 Meadows et al., 2010). The relative aridity of each sites is shown on the legend. Inset indicates
652 position of the region within the southwestern Cape.

653 **Figure 4:** Pakhuis Pass rock hyrax middens sampled for this study: **a)** PK08, 7 cm tool atop
654 midden for scale; **b)** collecting a portion of the PK08 midden; **c)** PK10-1 midden, 16 cm GPS unit
655 for scale.

656 **Figure 5:** Age-depth models for the PK08, PK10-1 and PK1173 rock hyrax middens.

657 **Figure 6:** Pane (a): The $\delta^{15}\text{N}$ data from the PK08 (red), PK10-1 (blue, sample location provided
658 for lower resolution Holocene portion) and PK1173 (green) rock hyrax middens. Pane (b): The
659 same records following corrections made to establish a single composite record for the site. The
660 PK10-1 midden is associated with a more exposed foraging range and thinner soils, and a
661 0.95‰ correction factor was applied based on average values from PK08 and PK1173
662 (recovered from more mesic locations) for overlapping time periods. For the >15,500 cal BP
663 portion of the sequence the similarly resolved, but irregularly sampled overlapping portions of
664 PK10-1 and PK1173 (dashed lines) have been combined (shown in black) using Gaussian kernel-

665 based interpolation (Rehfeld et al., 2011). The timing of major changes as identified from the
666 composite record using change point analysis (Killick et al., 2012) are indicated by vertical
667 dashed lines.

668 **Figure 7:** The $\delta^{15}\text{N}$ data from the Pakhuis Pass (this paper), De Rif (Chase et al., 2011) and
669 Seweweekspoort (Chase et al., 2017) rock hyrax middens, and the sea-salt sodium flux data
670 from the EPICA Dronning Maud Land ice core from Antarctica, a proxy for sea-ice extent
671 (Fischer et al., 2007).

672 **Figure 8:** Holocene $\delta^{15}\text{N}$ records from the Pakhuis Pass (this paper), Katbakkies Pass (Chase et
673 al., 2015b), De Rif (Chase et al., 2015a) and Seweweekspoort (Chase et al., 2017) rock hyrax
674 middens, as well as the afrotemperate forest pollen record from Eilandvlei (Quick et al., 2018),
675 and proxies records relating to the position of the southern westerlies, including
676 reconstructions of Southern Ocean summer sea-surface temperatures and sea ice presence
677 (Nielsen et al., 2004) and the sea-salt sodium flux data from the EPICA Dronning Maud Land ice
678 core from Antarctica, a proxy for sea-ice extent (Fischer et al., 2007; Roberts et al., 2017).

679 **Figure 9:** Holocene western Cape Floristic Region $\delta^{15}\text{N}$ records from the Pakhuis Pass (this
680 paper), Katbakkies Pass (Chase et al., 2015b) and De Rif (Chase et al., 2015a) rock hyrax
681 middens, resampled to a common 100-year resolution (linear interpolation). Three time slices
682 have been selected across the mid-Holocene (4600, 5600 and 7000 cal BP), and the $\delta^{15}\text{N}$ values
683 from the sites, as proxies for water availability, have been used to interpolate the steepness of
684 hydroclimatic ($\delta^{15}\text{N}$) gradients between the sites. White isolines are described at 0.2‰ $\delta^{15}\text{N}$
685 intervals. *Note, as only three sites were used in this calculation, extrapolated gradients not*

686 *along the vector described by these three sites should not be considered as reliable*
687 *reconstructions.*