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Orbital controls on Namib Desert hydroclimate over the past 50,000 years

Chase, B. M., Niedermeyer, E. M., Boom, A., Carr, A. S., Chevalier, M., He, F., Meadows, M. E., Ogle, N., & Reimer, P. J. (2019). Orbital controls on Namib Desert hydroclimate over the past 50,000 years. *Geology*, 47(9), 867. <https://doi.org/10.1130/G46334.1>

Published in:
Geology

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
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1 Extreme hydroclimate gradients within the western Cape
2 Floristic region of South Africa since the Last Glacial
3 Maximum

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17

18 **Abstract**

19 The Cape Floristic Region (CFR) is one of the world's major biodiversity hotspots, and much work
20 has gone into identifying the drivers of this diversity. Considered regionally in the context of
21 Quaternary climate change, climate stability is generally accepted as being one of the major
22 factors promoting the abundance of species now present in the CFR. However, little direct
23 evidence is available from the region, and responses to changes in global boundary conditions
24 have been difficult to assess. In this paper, we provide new high-resolution stable isotope data
25 from Pakhuis Pass, in the species-rich western CFR, and contextualise our findings through
26 comparison with other records from the region. Combined, they indicate clear, coherent changes
27 in regional hydroclimate, which we relate to broader forcing mechanisms. However, while these
28 climate change events share similar timings (indicating shared macro-scale drivers), the
29 responses are distinct between sites, in some cases expressing opposing trends over very short
30 spatial gradients (<50 km). We describe the evolution of these trends, and propose that while
31 long-term (10^5 yr^{-1}) general climatic stability may have fostered high diversity through low
32 extinction rates, the strong, abrupt changes in hydroclimate gradients observed in our records
33 from across the region may have driven a form of allopatric speciation pump, promoting the
34 diversification of plant lineages through the periodic isolation and recombination of plant
35 populations.

36 **Keywords**

37 Palaeoclimate, climate dynamics, South Africa, Cape Floristic Region, biodiversity, rock hyrax
38 middens, stable isotopes

39 **Highlights**

- 40 • New high resolution $\delta^{15}\text{N}$ data from rock hyrax middens from the western Cape Floristic
41 Region.
- 42 • Position of the southern westerlies apparent as a strong determinant of regional
43 hydroclimates.
- 44 • Significant, rapid changes in hydroclimate are revealed in the region.
- 45 • Opposing responses to shared climate change events establish highly variable climate
46 gradients.

47 **1 Introduction**

48 Southern African hydroclimate is primarily defined by the advection and precipitation of moisture
49 from tropical Atlantic and Indian Ocean sources during the austral summer (Figure 1). In contrast,
50 southwestern South Africa experiences a distinct, inverse rainfall regime. Seasonal expansions of
51 the circumpolar vortex and equatorward migration of the westerly storm track bring increased
52 precipitation during winter months, while displacements of the South Atlantic Anticyclone during
53 the summer intensify upwelling along the west coast, blocking the westward propagation of
54 easterly waves, generating strong summer drought in the region (Tyson, 1986; Tyson and
55 Preston-Whyte, 2000). During the Quaternary, southern Africa is thought to have been sensitive
56 to long-term changes in these tropical and temperate systems. Driven by changes in global
57 boundary conditions, tropical systems are invigorated during interglacial periods and temperate
58 systems exert increased influence during glacial periods (Chase et al., 2015a; Chase et al., 2017;
59 see Chase and Meadows, 2007; Chevalier, 2018; Cockroft et al., 1988; Quick et al., 2011; van
60 Zinderen Bakker, 1976).

61 This dynamic, which is thought to have become dominant in the Plio-Pleistocene (5.0 –
62 2.6 Ma) when trade wind-controlled upwelling was established as a dominant factor in the
63 regional climate system (Diekmann et al., 2003), has created a Mediterranean climate zone in
64 the southwestern Cape of South Africa (Figure 2). This climatic evolution has been a key factor in
65 fostering the development of the vegetation of the Cape Floristic Region (CFR), which is
66 remarkable for its high level of endemism and its species richness (Cowling, 1992; Goldblatt,
67 1978).

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

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

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

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

112 **1.1 Regional setting**

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

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

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

141 **2 Material and methods**

142 Middens for this study, PK08 and PK10-1 (Figure 4) were collected from the same ~400 m long,
143 15 m high cliff band (32.093°S, 19.065°E) as those described by Scott and Woodborne (2007a, b)
144 and were selected for their high hyraceum (crystallised urine) relative to faecal pellet content.
145 Apart from having greater structural integrity and less variable deposition rates, hyraceum
146 represents environmental conditions more clearly than samples containing faecal pellets, which
147 may potentially include a degree of dietary bias and often exhibit far more
148 discontinuous/irregular deposition (Chase et al., 2012). Sections of each midden were cut
149 perpendicular to the stratigraphy using an angle grinder and/or rotary impact hammer (Figure 4)
150 and transported back to the laboratory for analysis. In addition to these newly collected middens,
151 we analysed one of the Pakhuis Pass middens (PK1173) considered in the papers of Scott and
152 Woodborne (2007a, b)

153 **3 Chronology**

154 Radiocarbon age determinations for the PK08 and PK10-1 middens (n=14) were processed at the
155 ¹⁴CHRONO Centre, Queen's University Belfast using accelerator mass spectrometry (AMS) (Table
156 1; Figure 5). Samples were pre-treated with 2% HCl for one hour at room temperature to remove
157 carbonates and dried at 60°C. They were then weighed into quartz tubes with an excess of CuO,
158 sealed under vacuum and combusted to CO₂. The CO₂ was converted to graphite on an iron
159 catalyst using the zinc reduction method (Slota et al., 1987). The radiocarbon ages were corrected
160 for isotope fractionation using the AMS measured $\delta^{13}\text{C}$. These ages and those obtained from
161 PK1173 (Scott and Woodborne, 2007a) were calibrated using the SHCal13 calibration data (Hogg
162 et al., 2013). The Clam 2.2 software package (Blaauw, 2010) was used to generate all age-depth
163 models (Figure 5). Clam was chosen over Bayesian techniques such as Bacon (Blaauw and
164 Christen, 2011) because strong changes in accumulation rate may occur in hyrax middens (such
165 as PK08 and PK10-1), and Clam – using linear models - is better suited to such sequences.

166 **3.1 Stable nitrogen isotopes**

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

172 **4 Results**

173 **4.1 Chronology**

174 Radiocarbon analyses indicate that the Pakhuis Pass hyrax middens accumulated during the late
175 Pleistocene and Holocene, spanning the last ~19,300 years cal (calibrated) BP. The age-depth
176 models for the two middens suggest continuous deposition, although accumulation rates do vary
177 considerably (Table 1; Figure 5). Accumulation rates for the PK08 midden average ~28 $\mu\text{m yr}^{-1}$,
178 with a period of more rapid accumulation centred on 6000 cal BP (~132 $\mu\text{m yr}^{-1}$). Each 1 mm
179 isotope sample from PK08 therefore integrates between ~8 and 105 years of hyraceum
180 accumulation (averaging 42 mm yr^{-1}). Accumulation rates for the PK10-1 midden increase with
181 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.
182 Therein, each 1 mm isotope sample from PK10-1 integrates between ~380 years (upper section)
183 to ~10 years (lower section) of hyraceum accumulation. Because of this significant change in
184 accumulation rate, we show data from the extremely low resolution of the Holocene portion of
185 PK10-1, but do not consider it our analyses, favour the much more highly resolved record from
186 PK08. Accumulation of the PK1173 midden was more regular, averaging ~50 $\mu\text{m yr}^{-1}$, with each
187 isotope sample integrating ~20 years of accumulation.

188 **4.2 Stable nitrogen isotopes**

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

193 of this signal in plant and animal tissues and in faecal matter (e.g. Carr et al., 2016; Hartman,
194 2011; Murphy and Bowman, 2006; Newsome et al., 2011) has been demonstrated. This is thought
195 to be generally a function of a more open nitrogen cycle in arid regions. Fractionating pathways
196 in the soil (nitrification, denitrification, etc.) mean that nitrogen lost through transformation and
197 the release of gaseous products is depleted in ^{15}N , and the remaining nitrogen is enriched. While
198 in more humid regions N is cycled between live and dead organic pools, in drier regions more N
199 flows to mineral pools where it is subject to gaseous loss (Amundson et al., 2003), and the $\delta^{15}\text{N}$
200 value of soils is thus higher with increasing aridity (Austin and Vitousek, 1998; Handley et al.,
201 1999; Murphy and Bowman, 2009). The environmental processes relating to this recycling or loss
202 of ^{15}N are not tied exclusively to rainfall amount, but in climatic terms are more accurately
203 considered to relate to water availability (Murphy and Bowman, 2006). Studies of ^{15}N in hyrax
204 middens from a wide range of environments indicate consistently strong correlations between
205 midden ^{15}N , local vegetation/soil ^{15}N , as well as independent climate proxy records, supporting
206 the conclusion that environmental moisture availability is a major driver of midden ^{15}N records
207 (Carr et al., 2016; Chase et al., 2015a; Chase et al., 2013; Chase et al., 2017; Chase et al., 2015b;
208 Chase et al., 2010; Chase et al., 2009; Chase et al., 2011).

209 This general relationship may also be influenced to some extent by other (e.g.
210 microclimatic) factors, as is reflected in the variability observed in the relationship between
211 modern foliar ^{15}N and aridity estimates (e.g. Hartman and Danin, 2010; Murphy and Bowman,
212 2006; Peri et al., 2012). This influence can be observed in the offset between the PK08 and
213 PK1173 records and the record from PK10-1 (Figure 6). This is not uncommon when comparing
214 records from different middens, even when in relatively close proximity (<20 m). These

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

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

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

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

245 Using change point analysis (Killick et al., 2012; Trauth et al., 2018), major transitions in the
246 record (where the root-mean-square level of the signal changes most significantly) were
247 identified. Most notably, the period following the termination of early Holocene aridity at ~6800
248 cal BP is marked by a series of abrupt changes reflecting a rapid increase in water availability
249 between ~6800 and 6140 cal BP. This period of relatively humid conditions ends equally abruptly,
250 with distinctly drier conditions persisting from 5520 - 4480 cal BP. A subsequent sharp increase
251 in water availability is followed by a gradual aridification between 4480 and 2830 cal BP, and
252 apparently more stable conditions during the late Holocene. It is worth noting that the amplitude
253 of change registered across these transitions (as much as 4.5‰) is similar to the amplitude of
254 change between the Last Glacial Maximum and Holocene (5‰). Using the data derived from
255 modern hyrax faecal pellets presented by Carr et al. (2016), this may speculatively be translated
256 to a ~70% increase in water availability (Aridity Index from 0.25 to 0.42) for the period between

257 ~6800 and 6100 cal BP (Figure 6). Unfortunately, the midden records obtained do not provide
258 detailed information regarding modern/sub-modern conditions, and a full contextualisation of
259 these results in comparison with modern climates and recent change is not yet possible.

260 **5 Discussion**

261 **5.1 Glacial-interglacial scale variability**

262 Considering the combined influences of lower Pleistocene temperatures (Chevalier and Chase,
263 2015; Lim et al., 2016; Stute and Talma, 1998; Talma and Vogel, 1992), and the position of Pakhuis
264 Pass in the winter rainfall zone, which is considered to have received increased precipitation
265 during glacial periods (Chase et al., 2017; Chase and Meadows, 2007; Cockcroft et al., 1987; van
266 Zinderen Bakker, 1976), it is not surprising that the late Pleistocene is characterised by more
267 humid conditions (Figure 7). What is most remarkable about the Pakhuis Pass $\delta^{15}\text{N}$ record is that
268 it indicates dramatically different patterns of change than those recorded at the De Rif hyrax
269 midden site, located only 42 km to the south (Figure 2,3; Chase et al. 2011, 2015). This implies
270 past climate change dynamics characterised by marked levels of spatio-temporal heterogeneity.
271 Previously, inter-regional differences have been indicated by $\delta^{15}\text{N}$ records from Seweweekspoort
272 (Figure 2; 230 km east-southeast of De Rif). In isolation, the differences between the De Rif and
273 Seweweekspoort might otherwise have been explained by the distinct natures of eastern and
274 western CFR climate histories (Chase and Meadows, 2007; Cowling et al., 1992). The new data
275 from Pakhuis Pass imply a more complex dynamic.

276 Interpretations of the Seweweekspoort and De Rif records, which extend into the Last
277 Glacial Maximum (LGM; 19-26.5 ka (Clark et al., 2009)) have highlighted the influence of different

278 elements of the regional climate system as they were impacted by changing global boundary
279 conditions. At glacial-interglacial timescales, the $\delta^{15}\text{N}$ record from Seweweekspoort (Chase et al.,
280 2017) has been identified as primarily reflecting changes in the climate system related to global
281 temperature and Antarctic sea-ice, which has been hypothesised as being a significant control on
282 the position of the southern westerlies storm track (Chase and Meadows, 2007; Cockcroft et al.,
283 1987; van Zinderen Bakker, 1976). In contrast, at De Rif, despite being closer to the core of the
284 WRZ, where temperate systems define the modern regional rainfall regime, the primary control
285 on hydrologic balance at millennial and multi-millennial timescales appears to be variations in
286 the length and intensity of the summer drought season, potentially modulated by variations in
287 the intensity of the South Atlantic Anticyclone, which blocks the incursion of tropical air masses
288 and limits convection (Chase et al., 2015a). In the higher elevations of the Cederberg mountains,
289 while winter rainfall is consistent and abundant, changes in summer rainfall may have had a more
290 significant influence on driving drought-stress at the site. Including the new Pakhuis Pass $\delta^{15}\text{N}$
291 record in this regional consideration, it seems likely (based on similarities in first-order trends
292 with SWP, as well as EPICA Dronning Maud Land ice core sea-salt sodium flux record, considered
293 as a general proxy for sea-ice extent (Fischer et al., 2007)) that at glacial-interglacial timescales
294 conditions at Pakhuis Pass is predominantly impacted by changes in temperate system influence,
295 with summer rainfall playing a relatively limited role in defining water availability.

296 **5.2 The Holocene**

297 Focussing on the Holocene, more, and more precise data can be brought to bear on the question
298 of CFR climate dynamics. While data coverage remains far from comprehensive, high resolution
299 stable isotope data from rock hyrax middens have provided important clues as to some of the

300 drivers and spatial dynamics that have defined climate change in the region during the Holocene
301 (Figure 8). Building from the basis of the conceptual models developed by van Zinderen Bakker
302 (1976) and Cockcroft et al. (1987), which indicate that periods of global cooling (warming) will
303 generally result in wetter (drier) conditions in the WRZ (SRZ), and that a coeval inverse
304 relationship in terms of precipitation amount exists between the two regions, more nuanced
305 scenarios regarding observed variability are being proposed.

306 To constrain the relationship between CFR climate dynamics and the underlying drivers
307 of the observed variability, we have considered the diatom-based Atlantic sector sea-ice extent
308 and Southern Ocean summer sea-surface temperature (SSST) reconstructions of Nielsen et al.
309 (2004) from marine core TN057-17. Similarities with these records can be observed at sites across
310 the CFR, but it appears that the relationship between humidity and mid-latitude SSSTs changes
311 from positive to negative moving from the eastern to western CFR. At the coastal eastern CFR
312 site of Eilandvlei (Quick et al., 2018), for example, higher percentages of afrotemperate forest
313 pollen (considered to indicate increased humidity and reduced drought stress) correlate well with
314 higher SSSTs at TN057-17 (Figure 8). In contrast, higher humidity at Pakhuis and Katbakkies
315 passes are more clearly linked to lower SSSTs. Climatically, this most likely indicates that
316 increased westerly influence results in more humid conditions in the lee of the Cederberg
317 mountains, perhaps related to a greater frequency of more powerful frontal systems.

318 Considering the relationship between the Pakhuis and Katbakkies pass sites, the impact
319 of changes in westerly influence is variable even between these two sites, despite their proximity
320 and their shared position in the lee of the Cederberg. Katbakkies Pass $\delta^{15}\text{N}$ record exhibits

321 changes in both the timing and amplitude that are similar to changes in TN057-17 SSSTs, perhaps
322 indicating that variations in humidity are more tightly coupled to temperate frontal systems than
323 at Pakhuis Pass, where the timing and direction of the anomalies is shared, but the local response
324 is less consistent (Figure 8). As has been indicated (Chase et al., 2017), increased frontal activity
325 during the Holocene is not necessarily inconsistent with the increases in summer rain that have
326 been previous suggested to drive moisture availability at Katbakkies Pass (Chase et al., 2015b),
327 but it is clear that further work is required to adequately understand how temperate and tropical
328 systems interact to create precipitation events in the region on the timescales considered here.

329 Underscoring the regional heterogeneity and the variable influence of the region's
330 moisture bearing systems, the Holocene record from De Rif once again is markedly different from
331 the Pakhuis and Katbakkies pass sites (Figure 8). Whereas the Pakhuis and Katbakkies Pass
332 records exhibit a generally negative relationship between humidity and TN057-17 SSSTs, at De
333 Rif the relationship is generally positive, with more humid conditions occurring during periods of
334 relatively elevated SSSTs. In the early Holocene, while sea ice presence is low, conditions at De
335 Rif are at their most humid for the last 19,400 years. With cooling SSSTs and increased sea ice
336 presence after 7000 cal BP, conditions become significantly drier. This extreme change during
337 the early to mid-Holocene transition exemplifies the apparently sharply contrasting trends across
338 the region, with the records from both Pakhuis and Katbakkies pass showing a strong increase in
339 humidity evident from ~7000 – 6000 cal BP. While more muted, this coeval inverse relationship
340 between the Pakhuis and Katbakkies Pass sites and the De Rif persists throughout the Holocene,
341 indicating that conditions at all of the sites are controlled by a shared dynamic, but that opposing

342 factors determine conditions in the mountains (De Rif) and the rainshadow (Pakhuis and
343 Katbakkies passes).

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

352 We hypothesise that these changes in environmental gradients may have had a significant
353 influence on the diversity and distinction of environmental niches in the region, and that changes
354 in these gradients may have acted as locks for gene flow, serving to alternatively isolate or enable
355 the migration and mixing of plant species across the region. Considering the observation that
356 species richness in the western CFR is higher in montane regions, the data presented here provide
357 palaeoclimatic evidence that highly variable environmental gradients may have acted as a kind
358 of allopatric speciation pump (e.g. Goldblatt and Manning, 2002; Haffer, 1969; Linder, 1985;
359 Linder, 2003; Verboom et al., 2015), with the repeated isolation and mixing of promoting the
360 exceptionally high species diversity of the CFR.

361 Further work will be required to establish where and to what extent variability on the
362 scale discussed in this paper has been biologically significant. Has the degree or rate of change

363 exceeded the tolerance of specific plant species or their ability to migrate? Can the spatial
364 configuration of climate response anomalies be reliably linked to spatial patterns of species
365 richness? Or, are the changes observed in the records discussed largely insignificant, and play no
366 consequential role in determining species richness. Studies of fossil pollen records from the
367 region provide a mixed response, with some indicating only minor changes in vegetation
368 composition during the late Pleistocene and Holocene (Meadows et al., 2010; Meadows and
369 Sugden, 1991), while other indicate substantial changes in vegetation have occurred (Scott and
370 Woodborne, 2007a; Valsecchi et al., 2013). To adequately evaluate and compare these findings,
371 more sites from transects across the region will need to be studied using a consistent
372 methodology that employs a range of proxies capable of differentiating climate and vegetation
373 change, and assessing spatial patterns of genetic diversity.

374 **6 Conclusions**

- 375 • We present a new, high resolution $\delta^{15}\text{N}$ record from Pakhuis Pass in the Cederberg
376 Mountains of the western Cape Floristic Region.
- 377 • Like recently published records from the region (Chase et al., 2015a; Chase et al., 2015b),
378 the data from Pakhuis Pass indicate substantial, rapid changes in hydroclimatic
379 conditions, contrasting with earlier suggestions that the Cederberg experienced relatively
380 little environmental change during since the LGM (Meadows et al., 2010; Meadows and
381 Sugden, 1991).
- 382 • The record from Pakhuis Pass indicates similarities with patterns of change observed in
383 comparable records from Katbakkies Pass ((Chase et al., 2015b), also in the rainshadow

384 of the Cederberg) but contrasts sharply with conditions at De Rif (Chase et al., 2015a),
385 where a coeval inverse pattern of variability is observed. Commonalities in the *timing* of
386 change suggest a shared driver of regional climate dynamics, but distinct local responses,
387 perhaps as a function of orographic influences.

388 • The opposing regional responses indicate significant changes in environmental gradients
389 across the western CFR.

390 • While hydroclimatic conditions at Pakhuis Pass and De Rif may have been similar
391 immediately after the LGM, subsequent responses to changes in global boundary
392 conditions during deglaciation resulted in the establishment of a steep environmental
393 gradient between the sites.

394 • We hypothesise that changes in the slope of this gradient likely reflect similar patterns
395 across the region, and that these changes may have driven an allopatric speciation pump,
396 contributing to the elevated species diversity observed in the montane regions of the
397 western CFR.

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

401 **7 Acknowledgements**

402 The research leading to these results has received funding from the European Research Council
403 under the European Union's Seventh Framework Programme (FP7/2007-2013), ERC Starting

404 Grant "HYRAX", grant agreement no. 258657. We are very grateful to Louis Scott for providing a
405 portion of the PK1173 midden for analysis.

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608

609 **Table captions**

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

612 **Figure captions**

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

616 **Figure 2:** Map of southernmost Africa showing **A)** showing seasonality of rainfall and climatic
617 gradients defined in terms of percentage of winter rainfall, **B)** the extent of the vegetation types
618 comprising the Cape Floristic Region (fynbos, renosterveld and Albany Thicket (data from Mucina
619 and Rutherford, 2006)), **C)** a map of mean Aridity Index values for the region (Trabucco and
620 Zomer, 2009), and **D)** a map of species richness using data derived from the GBIF database
621 (Chevalier, 2019; 2018; GBIF.org, 2018, b, c, d, e, f, g, h); number of species per quarter-degree
622 grid cell were interpolated to create the contour map. Classification of aridity values follows that
623 of the United Nations Environment Programme (1997). Sites considered in this study are
624 indicated: Pakhuis Pass (PK: this study; Scott and Woodborne, 2007a; Scott and Woodborne,
625 2007b), De Rif (DR: Chase et al., 2015a; Chase et al., 2011; Quick et al., 2011), Katbakkies Pass
626 (KB: Chase et al., 2015b; Meadows et al., 2010), Seweweekspoort (SWP: Chase et al., 2015a;
627 Chase et al., 2013; Chase et al., 2017) and Eilandvlei (Quick et al., 2018).

628 **Figure 3:** Map of the N-S axis of the Cape Fold Mountains in the southwestern Cape, including
629 the Cederberg Mountains and adjacent ranges. Topographic variability is overlain by a map of
630 mean Aridity Index values (Trabucco and Zomer, 2009) for the region, as in Figure 1. The
631 dominant vector of temperate moisture-bearing systems related to the westerly storm track is
632 shown, as are the sites considered in this study: Pakhuis Pass (this study; Scott and Woodborne,

633 2007a; Scott and Woodborne, 2007b), De Rif (Chase et al., 2015a; Chase et al., 2011; Quick et al.,
634 2011), Katbakkies Pass (Chase et al., 2015b; Meadows et al., 2010). The relative aridity of each
635 sites is shown on the legend. Inset indicates position of the region within the southwestern Cape.

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

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

639 **Figure 6:** Pane (a): The $\delta^{15}\text{N}$ data from the PK08 (red), PK10-1 (blue, sample location provided for
640 lower resolution Holocene portion) and PK1173 (green) rock hyrax middens. Pane (b): The same
641 records following corrections made to establish a single composite record for the site. The PK10-
642 1 midden is associated with a more exposed foraging range and thinner soils, and a 0.95‰
643 correction factor was applied based on average values from PK08 and PK1173 (recovered from
644 more mesic locations) for overlapping time periods. For the >15,500 cal BP portion of the
645 sequence the similarly resolved, but irregularly sampled overlapping portions of PK10-1 and
646 PK1173 (dashed lines) have been combined (shown in black) using Gaussian kernel-based
647 interpolation (Rehfeld et al., 2011). The timing of major changes as identified from the composite
648 record using change point analysis (Killick et al., 2012) are indicated by vertical dashed lines.

649 **Figure 7:** The $\delta^{15}\text{N}$ data from the Pakhuis Pass (this paper), De Rif (Chase et al., 2011) and
650 Seweweekspoort (Chase et al., 2017) rock hyrax middens, and the sea-salt sodium flux data from
651 the EPICA Dronning Maud Land ice core from Antarctica, a proxy for sea-ice extent (Fischer et al.,
652 2007).

653 **Figure 8:** Holocene $\delta^{15}\text{N}$ records from the Pakhuis Pass (this paper), Katbakkies Pass (Chase et al.,
654 2015b), De Rif (Chase et al., 2015a) and Seweweekspoort (Chase et al., 2017) rock hyrax middens,
655 as well as the afrotemperate forest pollen record from Eilandvlei (Quick et al., 2018), and proxies
656 records relating to the position of the southern westerlies, including reconstructions of Southern
657 Ocean summer sea-surface temperatures and sea ice presence (Nielsen et al., 2004) and the sea-
658 salt sodium flux data from the EPICA Dronning Maud Land ice core from Antarctica, a proxy for
659 sea-ice extent (Fischer et al., 2007; Roberts et al., 2017).

660 **Figure 9:** Holocene western Cape Floristic Region $\delta^{15}\text{N}$ records from the Pakhuis Pass (this paper),
661 Katbakkies Pass (Chase et al., 2015b) and De Rif (Chase et al., 2015a) rock hyrax middens,
662 resampled to a common 100-year resolution (linear interpolation). Three time slices have been
663 selected across the mid-Holocene (4600, 5600 and 7000 cal BP), and the $\delta^{15}\text{N}$ values from the
664 sites, as proxies for water availability, have been used to interpolate the steepness of
665 hydroclimatic ($\delta^{15}\text{N}$) gradients between the sites. White isolines are described at 0.2‰ $\delta^{15}\text{N}$
666 intervals. *Note, as only three sites were used in this calculation, extrapolated gradients not along*
667 *the vector described by these three sites should not be considered as reliable reconstructions.*