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Seasonal availability of edible underground and aboveground carbohydrate resources to human foragers on the Cape south coast, South Africa

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The coastal environments of South Africa's Cape Floristic Region (CFR) provide some of the earliest and most abundant evidence for the emergence of cognitively modern humans. In particular, the south coast of the CFR provided for hunter-gatherers a uniquely diverse resource base, namely marine shellfish, game, and carbohydrate-bearing plants, especially those with underground storage organs (USOs). It has been hypothesized that these resource underpinned the continuity of human occupation in the region since the Middle Pleistocene. Very little research has been conducted on the foraging potential of carbohydrate resources in the CFR. This study focuses on the seasonal availability of plants with edible carbohydrate by assessing their visibility to foragers at six-weekly intervals over a two-year period in four vegetation types on South Africa's Cape south coast. A total of 52 edible plant species were recorded across all vegetation types. Of these, 33 species were geophytes with edible USOs and 21 species had aboveground edible carbohydrates. Limestone Fynbos had the richest flora, followed by Strandveld, Renosterveld and lastly, Sand Fynbos. The availability of USO species differed across vegetation types and between survey years. The number of available USO species was highest for a six-month period from winter to early summer (Jul-Dec) across all vegetation types. Months of lowest species' availability were in mid-summer to early autumn (Jan-Apr); the early winter (May-Jun) values were variable, being highest in Limestone Fynbos. However, even during the late summer carbohydrate "crunch", 25 carbohydrate bearing species were visible across the four vegetation types. Overall, the plant-based carbohydrate resources available to Stone Age foragers of the Cape south coast, especially USOs belonging to the Iridaceae family, are likely to have comprised a reliable and nutritious source of calories over most of the year. The winter and early spring months likely coincided with a scarcity of protein, especially marine invertebrates, but an abundance of carbohydrates. At these times, plant carbohydrates, especially USOs, may have comprised 100% of dietary intake. However, recognising which vegetation types are most productive, identifying hotspots of productivity and distinguishing between edible and toxic USOs must have required considerable cognitive skills.

1 **Seasonal availability of edible underground and aboveground carbohydrate**
2 **resources to human foragers on the Cape south coast, South Africa**

3

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34 **Abstract**

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36 The coastal environments of South Africa's Cape Floristic Region (CFR) provide some of the
37 earliest and most abundant evidence for the emergence of cognitively modern humans. In
38 particular, the south coast of the CFR provided for hunter-gatherers a uniquely diverse resource
39 base, namely marine shellfish, game, and carbohydrate-bearing plants, especially those with
40 underground storage organs (USOs). It has been hypothesized that these resource underpinned
41 the continuity of human occupation in the region since the Middle Pleistocene. Very little
42 research has been conducted on the foraging potential of carbohydrate resources in the CFR.
43 This study focuses on the seasonal availability of plants with edible carbohydrate by assessing
44 their visibility to foragers at six-weekly intervals over a two-year period in four vegetation types
45 on South Africa's Cape south coast. A total of 52 edible plant species were recorded across all
46 vegetation types. Of these, 33 species were geophytes with edible USOs and 21 species had
47 aboveground edible carbohydrates. Limestone Fynbos had the richest flora, followed by
48 Strandveld, Renosterveld and lastly, Sand Fynbos. The availability of USO species differed
49 across vegetation types and between survey years. The number of available USO species was
50 highest for a six-month period from winter to early summer (Jul-Dec) across all vegetation types.
51 Months of lowest species' availability were in mid-summer to early autumn (Jan-Apr); the early
52 winter (May-Jun) values were variable, being highest in Limestone Fynbos. However, even
53 during the late summer carbohydrate "crunch", 25 carbohydrate bearing species were visible
54 across the four vegetation types. Overall, the plant-based carbohydrate resources available to
55 Stone Age foragers of the Cape south coast, especially USOs belonging to the Iridaceae family,
56 are likely to have comprised a reliable and nutritious source of calories over most of the year.
57 The winter and early spring months likely coincided with a scarcity of protein, especially marine
58 invertebrates, but an abundance of carbohydrates. At these times, plant carbohydrates, especially
59 USOs, may have comprised 100% of dietary intake. However, recognising which vegetation
60 types are most productive, identifying hotspots of productivity and distinguishing between edible
61 and toxic USOs must have required considerable cognitive skills.

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Introduction

The Cape south coast has likely been occupied by hominins for at least the last 1 million years and the earliest archaeological remains attributable to *Homo sapiens* dates to approximately 160,000 years ago (Jerardino & Marean, 2010). Some of the earliest evidence for the emergence of complex behaviours associated with cognitively modern humans is found in this region, making it highly significant to human origins studies (Marean et al., 2014). The archaeological record on the Cape south coast for the period between 160,000 and 50,000 years, a time crucial to our understanding of modern human origins, is unusually data rich and well dated. It documents human occupation during periods of glacial maxima, such as Marine Isotope Stages 6 and 4, when climatic conditions over much of the rest of Africa were too harsh for human occupation or could sustain only very small populations. It has been hypothesised that the richness of the record and continuity of occupation along the Cape south coast, and the Cape Floristic Region (CFR) more generally, is a consequence of an unusually rich resource base unique to this area (Parkington 2001, 2003, 2006; Marean, 2010, 2011). The coastline in this region offers a highly productive inter-tidal zone for shellfish collection for human foragers. During glacial phases, an extensive plain was exposed off the current coast that supported a diverse plains game fauna, which would have offered excellent hunting opportunities (Klein, 1983; Marean, 2010). The CFR is also home to a globally exceptional flora with many species offering harvestable edible carbohydrates (Deacon, 1970, Parkington & Poggenpoel, 1971; Van Wyk & Gericke, 2000; Van Wyk, 2002; Schwegler, 2003; Dominy et al., 2008; De Vynck, Van Wyk & Cowling, in press). These include geophytic underground storage organs (USOs) that are both highly diverse and locally abundant (Goldblatt, 1978; Procheş, Cowling & du Preez, 2005; Procheş et al., 2006; E. Singels et al., unpublished data), as well as many species with aboveground carbohydrates such as fruit, vegetables, seed pods and seeds (De Vynck, Van Wyk & Cowling, in press). Together these resources may have provided a complementary set of protein and carbohydrate-rich foods to a human forager, thus explaining the continuity of human occupation through glacial maxima.

93 However, to date the actual productivity of these potential food resources to a human forager has
94 been largely based on conjecture. For example, Marean's (2010) argument that CFR geophyte
95 diversity directly resulted in a wide range of collectable plant foods would not hold if most of
96 those plants were poisonous, very low in caloric returns, very costly to procure, or unavailable
97 for large parts of the year. To better understand the record for hunter-gatherer foraging in this
98 region, we must develop robust understandings of the foraging potential of the plant foods. This
99 includes analyses of their nutritional character (Kyriacou et al., 2014), availability in the
100 landscape, overall return rates when harvesting (Singels et al. unpublished data), and
101 importantly their seasonal "visibility", and thus availability, to a forager looking to initiate a
102 foraging effort.

103
104 This study focuses on the seasonal availability of edible carbohydrate from a range of plant
105 species in four vegetation types on South Africa's Cape south coast. The ultimate goal is to
106 combine these observations with studies of nutrition and return rates, so as to contribute to the
107 resourcescape for a paleoscape model for the Cape south coast (Marean et al., 2015). More
108 generally, our paper adds to a growing literature on the importance of geophytes and
109 aboveground carbohydrates to hunter-gatherer diet worldwide (Kaye and Moodie, 1978; Hatley
110 & Kappelman, 1980; Vincent, 1985; Murray et al., 2001; Bliege Bird & Parker, 2005; Bliege
111 Bird et al., 2008), and expands the range of variation of those data to a region that is megadiverse
112 in plant species yet relatively unstudied in regards to plants, and geophytes in particular, as a
113 food resource.

114 115 **Methods**

116 117 **Study area**

118
119 The study area is situated in the coastal plain between the Breede and Gouritz rivers on the Cape
120 south coast (Fig. 1). The rainfall regime shows little seasonality and rain may fall at any time of
121 the year although slight rainfall peaks are observed in March–April and with more pronounced

122 peaks during August and October–November (Engelbrecht et al., 2014). The overall climate of
123 the study area is semi-arid to sub-humid with annual rainfall ranging from 350 to 550 mm. The
124 three summer months (Dec-Feb) are the most stressful for plant growth, owing to generally
125 lower rainfall and persistently higher temperatures.

126

127 **[Fig. 1 here]**

128

129 Vegetation of the Cape coastal lowlands is under strong edaphic control (Thwaites & Cowling,
130 1988; Rebelo et al., 1991) and the study area has a wide range of geologies which generate
131 different soil types. These include Table Mountain Group sandstones (visible on the coast),
132 Bokkeveld shales (exposed on the inland margin of the study area), Cretaceous Enon Formation
133 conglomerates and mudstones (~25 km from the coast), and Bredasdorp Formation limestones
134 (Rogers, 1984; Malan, 1987). In addition, near the coastal margin aeolian sands of marine origin
135 mantle the geology and this varies in pH with age; younger sands are alkaline and older sands are
136 leached and acidic (Rebelo et al., 1991; Abanda, Compton & Hannigan, 2011). Shale- and
137 mudstone-derived soils are moderately fertile, while those associated with leached sands are
138 infertile. The calcareous sands associated with limestone, calcrete and coastal dunes are also
139 relatively infertile due to their high alkalinity and subsequent low levels of plant-available
140 phosphorus (Thwaites & Cowling, 1988).

141

142 This study focussed on monitoring plots located in Renosterveld, Sand Fynbos, Limestone
143 Fynbos, and Strandveld. Renosterveld occurs on the relatively fertile and fine-grained soils
144 derived from shales and mudstones, and is a fire-prone grassy shrubland often dominated by
145 *Elytropappus rhinocerotis* (renosterbos). Sand Fynbos occurs on infertile acid soils and is a fire-
146 prone heath-like shrubland, characterised by the presence of Restionaceae and Proteaceae.
147 Limestone-derived soils support Limestone Fynbos, a highly endemic-rich vegetation type
148 (Willis et al., 1996). Marine sands are associated with subtropical thicket, either in its solid form
149 or as thicket clumps in a matrix of Fynbos. This vegetation is colloquially known as Strandveld.
150 Plant compositional change, or beta diversity, between these edaphically differentiated
151 vegetation types is extremely high; consequently few species are shared among these four
152 vegetation types and regional-scale plant richness is very high (Cowling, 1990).

153

154 **Data collection**

155

156 Four monitoring plots were located in representative areas of each of the major vegetation types
157 described above: Renosterveld, Sand Fynbos, Limestone Fynbos, and Strandveld (Fig. 1). These
158 plots were located within protected areas and were considered to be in a pristine condition.

159 Further biophysical data for the plots are provided in Table S1. The Sand Fynbos site had burnt
160 four years before the start of the survey period and this would likely have enhanced the visibility
161 of USO species (Deacon, 1993), many of which flower more profusely in the early post-fire
162 years (Le Maitre & Midgley, 1992).

163

164 Each plot was divided into six 20 × 300 m transects (3.6 ha in total). Monitoring consisted of
165 surveying each plot every six weeks over a two-year period. Along each transect we counted the
166 number of: 1) individuals of species bearing underground storage organs (USOs) which would
167 be apparent to a forager (i.e. in a phenophase where one or more aboveground organs were
168 visible) and, 2) individuals of species with edible aboveground carbohydrates; this included
169 fruits, leaves, seed pods, seeds, and inflorescences. In our sampling approach we adopted a
170 forager's perspective by only including species known to be edible (De Vynck, Van Wyk &
171 Cowling, in press) and excluding any plants considered too small to harvest. We included as
172 edible any USOs that required cooking in order to render them edible (e.g. tubers of *Rhoicissus*
173 *digitata* and corms of *Chasmanthe aethiopica* and *Watsonia* spp.) (Wells, 1965; Parkington &
174 Poggenpoel, 1971; Deacon, 1976, 1979; Liengme, 1987; Opperman & Heydenrych, 1990;
175 Skead, Manning & Anthony, 2009).

176

177 In the year prior to monitoring (2009), the rainfall was far below average across all plots (~70%
178 of the mean annual rainfall). Monitoring started in May 2010 and the effects of the previously
179 dry year were still evident. Above average rainfall was experienced over the two years of
180 monitoring (Fig. S1).

181

182 **Data analysis**

183

184 The relative availability of edible carbohydrates from each species within a plot over time was
185 calculated as the number of observed individuals for a given survey divided by the maximum
186 number of individuals observed across all surveys. For this calculation, individuals were only
187 included if they offered some form of edible carbohydrate (e.g. fruit, seed, tuber). The relative
188 availability of edible carbohydrates for each species was converted into a binary presence or
189 absence category using a 10% threshold, i.e. we considered a species readily visible and
190 available in the landscape if at least 10% of the maximum observed individuals were recorded.

191 The number of species with edible carbohydrate considered available in each plot through time
192 was calculated.

193

194 We used hierarchical clustering (Anderberg, 1973) to investigate patterns of phase synchronicity
195 (i.e. phenological timing) among edible USOs and fruiting species. Such clustering requires a
196 dissimilarity matrix as the input. Dissimilarity was calculated as the sum of the absolute
197 differences of relative visibility between two species (including site combinations, e.g. species 1
198 at site 1 versus species 1 at site 2, or species 1 at site 1 versus species 2 at site 1) for each survey
199 date. Hierarchical clustering was performed using the *hclust* function (Pinheiro et al., 2012) and
200 the averaging agglomeration method in R version 2.15 (R Development Core Team, 2014).

201 Defining clusters was not performed using a strict dissimilarity threshold, but rather involved
202 intuitive exploration of the phenograms of different potential clusters while endeavouring to
203 maintain cluster thresholds that were fairly similar.

204

205 **Results**

206

207 Within the four 3.6 ha plots spread across the four vegetation types, 52 edible plant species were
208 recorded. Of this, 33 species were geophytes with edible underground storage organs (USOs)
209 and 21 species had aboveground edible carbohydrates (Table 1; see Table S2 for full species list
210 per type). Note that some species had more than one edible part. Richness of edible species

211 varied across the vegetation types (Table 1): Limestone Fynbos had the richest flora, followed by
212 Strandveld, Renosterveld and lastly, Sand Fynbos.

213

214 **[Table 1 here]**

215

216 Species varied in their length of time they were available through the year (Fig. 2). Species with
217 USOs were available for longer periods of the year relative to those with edible aboveground
218 carbohydrates. The availability of USO species differed across vegetation types and between
219 survey years (Fig. 3). Nonetheless, the number of available USO species was highest for a six-
220 month period from winter to early summer (Jul-Dec) across all vegetation types. Months of
221 lowest species' availability were in mid-summer to early autumn (Jan-Apr); the early winter
222 (May-Jun) values were variable, being highest in Limestone Fynbos. In the wetter second year,
223 the summer “crunch” period – where few USO species were available – was at least one month
224 shorter than in the first year. The number of species with available edible aboveground
225 carbohydrates also varied across vegetation types and sample years. Species richness peaked in
226 spring (Sep-Nov) for all vegetation types; relatively high availability extended into summer
227 (Dec-Feb) but autumn and early winter were lean months for harvesting aboveground
228 carbohydrates in all vegetation types, especially Renosterveld and Sand Fynbos. The presence of
229 two *Carpobrotus* species, which bear ripe fruits during the drier months, was a key factor for the
230 extension of aboveground availability period in Limestone Fynbos.

231 An impressive 25 species provided edible carbohydrate during the late summer (Feb – Mar)
232 “crunch period (Table 2). Twelve of these were USOs and Limestone Fynbos supported the
233 most species (16) with carbohydrate on offer at this time.

234

235 **[Fig. 2 here]**

236 **[Fig. 3 here]**

237 **[Table 2 here]**

238

239 The multivariate analysis categorised seven phenophases of availability for edible underground
240 and aboveground carbohydrates across the plots (A to G; Fig. 4). Most phenophases comprised a
241 combination of underground and aboveground carbohydrate species as well as species found in
242 at least three, often all four, vegetation types. Exceptions are the summer phenophase (B), which
243 consisted entirely of aboveground carbohydrate species predominantly from Limestone Fynbos,
244 and the extended autumn-to-summer phenophase (D), which only has species with underground
245 storage organs.

246

247 [Fig. 4 here]

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251 Discussion

252

253 Substantial archaeological evidence exists for the use of underground storage organs (USOs),
254 fruits and leaves by Late Stone Age peoples in southern Africa (Deacon & Deacon, 1963;
255 Parkington & Poggenpoel, 1971; Deacon, 1970, 1976, 1984; Opperman & Heydenrych, 1990;
256 Deacon & Deacon, 1999) This evidence is substantiated by direct observations of contemporary
257 hunter-gatherer communities in Africa (Lee, 1969, 1973, 1984; Berbesque & Marlowe, 2009;
258 Marlowe & Berbesque, 2009). The diversity and abundance of edible plants, especially USOs,
259 along the Cape coast, together with a rich source of both marine and terrestrial based protein, has
260 been hypothesised to be key components facilitating the persistence of Middle Stone Age (MSA)
261 people in the region during glacial phases when other African regions may have been resource
262 poor (Marean, 2010). However, very little research has been conducted on the potential
263 availability of food plants to hunter-gatherers on the Cape south coast to corroborate this
264 hypothesis. In the same study area, Singels et al. (unpublished data) found surprisingly high
265 edible biomass values for USOs (maximum values range from 600 kg/ha in Sand Fynbos to
266 5 000 kg/ha in Limestone Fynbos), although these were restricted to occasional biomass hotspots
267 within a matrix of much lower biomass. In addition, these USO hotspots were found within all
268 vegetation types. Here we address the temporal availability of belowground (i.e. USOs) and
269 aboveground sources of carbohydrates across the four principal vegetation types of the Cape
270 south coast. We use this to speculate on the importance of carbohydrates as fallback foods for

271 coastal hunter-gatherers, and what role this may have played in the emergence of cognitively
272 modern people in the region (Marean, 2010).

273

274

275 The number of species with edible carbohydrate resources that are visible and available to
276 foragers was highest between winter and early summer in the study area. This is consistent with
277 the dominant cool-season phenology of plants in the Cape Floristic Region (Pierce, 1984). This
278 six-month period provides a diversity of USOs associated with corms belonging to petaloid
279 geophytes, mostly members of the Iridaceae (e.g. *Babiana*, *Freesia*, *Gladiolus*, *Watsonia*). These
280 species provide relatively large (10-100 g) starch-rich and low-fibre food parcels that are
281 inexpensive to harvest (Parkington, 1977; Deacon, 1993; Singels et al., unpublished data), and
282 many do not require cooking for digestion (Dominy et al., 2008; J. De Vynck pers. obs., 2011).
283 Also available during the cooler and mostly wetter months are fruits borne largely by subtropical
284 thicket species (e.g. *Carissa*, *Diospyros*, *Olea*, *Searsia*) as well as leaf crops (*Trachyandra* spp.).
285 There are currently no data on the biomass, nutritional value and foraging returns for
286 aboveground sources of carbohydrate in the Cape Floristic Region. Fruit loads of mature thicket
287 shrubs and trees range from tens of thousands of fruits per plant for *Sideroxylon inerme* (fruit
288 diameter 10 mm) and *Searsia* spp (3 mm) to fewer than 100 fruits for *Euclea racemosa* (7 mm),
289 *Cassine tetragona* (8 mm) and *Osyris compressa* (20 mm) (Cowling et al., 1997). Mat-forming
290 *Carpobrotus* species may bear several tens of large (35 mm diameter) fruits (J. De Vynck pers.
291 obs., 2011).

292

293 Late summer to early autumn have considerably fewer available edible species than in the other
294 times of the year. This is a period when all traces of leaves and inflorescences of the dominant
295 deciduous geophyte component have disappeared (Deacon, 1993). However, even during this
296 relatively warm and dry period, we recorded some 25 available species across the four vegetation
297 types (Table 2). These include USOs such as hysteroanthous, autumn-flowering *Gladiolus*
298 (cormous) and *Pelargonium* (tuberous) spp, the corms of evergreen *Watsonia* spp., and the
299 fibrous tubers of the evergreen liana, *Rhoicissus digitata*. Also apparent are the fruits
300 *Carpobrotus* spp, the fruits of many subtropical shrubs and trees, and the leaf crop, *Tetragonia*
301 *decumbens*. Nonetheless, the late summer – early autumn months could represent a carbohydrate

302 “crunch” for foragers: at this time the number of edible plant species is at its lowest and the high-
303 biomass items available to foragers (e.g. *Pelargonium* spp., *R. digitata*) are fibrous and require
304 cooking for digestion (Deacon, 1995; Dominy et al., 2008).

305

306

307 Overall, the plant-based carbohydrate resources available to Stone Age foragers of the Cape
308 south coast, especially USOs belonging to the Iridaceae (Deacon, 1976, 1993; Dominy et al.,
309 2008), are likely to have comprised a reliable and nutritious source of calories over most of the
310 year. Moreover, availability of USOs showed little between-year variation, most likely due the
311 existence of sufficient storage reserves to enable at least leaf growth every year (Ruiters and
312 McKenzie, 1994) despite variation in rainfall. In an assessment of foraging potential of six USO
313 species growing in our study area, Singels et al. (unpublished data) showed that 50% of foraging
314 events conducted yielded enough calories to meet the daily requirements of a hunter-gatherer of
315 small stature within two hours.

316

317 The juxtaposition within a 10 kilometre foraging radius of four major vegetation types,
318 belonging to three regional biomes (Fynbos, Renosterveld and Thicket; Bergh et al., 2014),
319 would have enabled humans to forage in very different resourcescapes on a daily basis. While
320 the Limestone Fynbos and Strandveld – the two vegetation types closest to the coast – are likely
321 to have offered the best foraging returns for much of the year, Renosterveld provides an
322 abundance of Iridaceae corms in the spring and Sand Fynbos harbours evergreen *Watsonia* spp.,
323 which can be harvested during the late summer-autumn “crunch” (Singels et al. unpublished
324 data). Ethnographic evidence suggest that the harvesting of Iridaceae corms (*uintjies*) in spring
325 was an important event for the San of the Cape west coast (Van Vuuren, 2014).

326

327 Given the temporal and spatial availability of edible plant species in the Cape, we argue that is
328 highly likely that USOs, fruit, seedpods, seeds, inflorescences and leaf crops were harvested as
329 fallback foods by Stone Age people living in this region. The preferred food for south Cape
330 coastal hunter-gatherers comprised the region’s diverse and abundant marine resources (Marean
331 et al., 2007; Jerardino & Marean, 2010; Parkington, 2010), and a diverse ungulate plains fauna,
332 including in the Pleistocene, several species of now extinct megafauna, associated with the

333 submerged Agulhas Bank (Klein, 1983; Parkington, 2001, 2003; Matthews, Marean & Nilssen,
334 2009; Marean, 2010; Faith, 2011). However, these resources were not always available to
335 harvesters and hunters, and the contraction and expansion of the Agulhas Plain ecosystem and its
336 ungulate communities must have been a major driver of changing foraging patterns on the south
337 coast (Marean et al., 2014). It has been hypothesized that the mammal fauna formed a migratory
338 community that moved west during the winter rains and east to intercept the summer rains.
339 Thus, the local abundance of many of the larger ungulates may have plummeted during the
340 winter months when populations migrated west to graze winter-growing grasses of the west
341 coast. Marine invertebrates, harvested from the intertidal, comprised the most reliable and
342 accessible source of protein for hunter-gatherers living on the Cape south coast (Marean, 2011).
343 Evidence for their use has been found in MSA sites such as Pinnacle Point (PP) 13B dating back
344 to ~160 ka (Marean et al., 2007; Jerardino & Marean, 2010) and at early modern human sites that
345 date between 110-50 ka such as Blombos Cave (Henshilwood et al., 2001; Langejans et al.,
346 2012), and Klasies River Mouth (Voigt, 1973; Thackeray, 1988). Late Stone Age sites suggest an
347 increase in the intensity of intertidal foraging (Marean et al., 2014) and indications of resource
348 depletion (Klein & Steele, 2013). Using experienced foragers of Khoe-San descent, J. De Vynck
349 et al. (unpublished data) showed exceptionally high peak return rates ($\sim 4,500$ kcal hr⁻¹) from the
350 Cape south coast intertidal under ideal harvesting conditions. However, owing to tidal
351 constraints, and the fierce sea conditions experienced there, harvesting was only possible for 10
352 days a month, for 2-3 hours on each day; lowest returns were recorded in winter and spring – a
353 time of strong winds and high seas – and highest returns in summer and autumn, when sea
354 conditions were calmer (J. De Vynck et al., unpublished data). Consequently, there would have
355 been periods of various lengths – ranging from days to weeks – when hunter-gatherers depended
356 on, or fell back upon carbohydrates for sustenance. As pointed out above, the winter and early
357 spring months likely coincided with a scarcity of protein but an abundance of carbohydrates. At
358 these times, plant carbohydrates, especially USOs, may have comprised 100% of dietary intake,
359 which would categorise them as a staple fallback food (Marshall & Wrangham, 2007).
360
361 It has been hypothesized that the persistence of a small group of hominins on the Cape south
362 coast – as opposed to their widespread extinction elsewhere in Africa during Marine Isotope
363 Stage 6 (MIS6, 193 000 -125 000 BP) (Foley, 1998; Lahr & Foley, 1998; Fagundes et al., 2007;

364 Basell, 2008; Masson-Delmotte et al., 2010) – was a consequence of the Cape’s relatively
365 moderate climate during the largely glacial MIS6 and its rich and diverse resource base. The
366 persistently warm Agulhas Current reduced the regional impact of glacial cooling substantially
367 (Negre et al., 2010; Zahn et al., 2010). Marean (2010) has hypothesised that during strong glacial
368 environments, such as those experienced in MIS6, the Cape south coast provided a unique
369 juxtaposition of resources important for hominin persistence, namely a diverse USO flora and a
370 rich and productive marine ecosystem. At that time the exposed Agulhas Plain (Fisher, Barr-
371 Matthews & Marean, 2010) was mantled in substrata that likely supported Limestone Fynbos
372 and Strandveld (Cawthra et al., 2015), offering a wide array of USOs, fruit and leaf crops which
373 would comprise reliable fallback foods when it was not possible to forage in the intertidal and
374 game was scarce. The cognitive challenges of exploiting marine resources (e.g. comprehending
375 lunar cycles), and defending them against competition from adjacent groups, led to a coastal
376 adaptation that may have contributed to the emergence of *Homo sapiens* (Marean, 2011).
377 Similarly, the ability to recognise which and when vegetation types are most productive for
378 carbohydrates, identifying hotspots of productivity and distinguishing between edible and toxic
379 USOs, must have required considerable cognitive skills (Deacon, 1995). The Cape is
380 megadiverse and diversity is hard to master.

381
382 Here we have established the temporal availability of plant species with edible carbohydrates
383 across four dominant vegetation types along the south coast. Much additional research must be
384 done to evaluate more comprehensively the role of above- and belowground carbohydrates in the
385 ecology and evolution of the human lineage in the Cape Floristic Region and elsewhere. Work is
386 currently underway to establish the return rates of carbohydrate resources harvested by
387 contemporary subjects of Khoe-San descent, in the different vegetation types and in different
388 seasons; and on the rates of depletion of resources in successively harvested areas. This needs to
389 be complemented with data on the nutritional value of the consumed parts of the species
390 selected. Ultimately, we aim to use these data to populate the carbohydrate resourcescape in an
391 agent-based model aimed at predicting the effects of spatial and temporal variability – governed
392 by changes in climate and the resource base over the seasonal cycle as well as the glacial-
393 interglacial cycle of the Pleistocene – on the population size and structure, mobility, social
394 organization, territoriality, and technology of Cape hunter-gatherers (Marean et al., 2015).

395

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397

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699 Table 1: Summary of edible species in 3.6 ha plots situated in four dominant vegetation types
700 along the Cape south coast.

	USOs	Fruit	Other ¹	All
Renosterveld	8	6	2	16
Sand Fynbos	5	4	1	10
Limestone Fynbos	21	11	7	39
Strandveld	15	8	5	28
Across all types ²	33	14	8	52

701 ¹ 'Other' includes species with edible: seed pods, seeds, leaves, and inflorescences.

702 ² Note that this is the number of unique species (i.e. some species are shared between vegetation types or
703 have more than one edible part).
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707 Table 2: Species available during the 'carbohydrate-crunch' late summer period (February-
708 March) in both survey years.

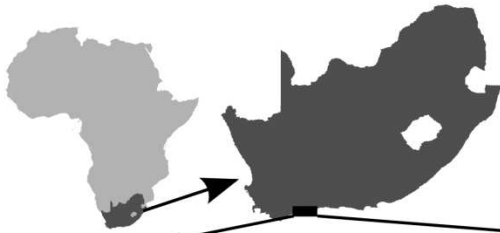
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Vegetation type	Carbohydrate category	Species
Renosterveld	Underground storage organ	<i>Babiana patula</i> ; <i>Cyphia digitata</i> ; <i>Watsonia meriana</i>
	Aboveground	<i>Diospyros dichrophylla</i> (fruit); <i>Osyris compressa</i> (fruit); <i>sideroxylon inerme</i> (fruit)
Limestone Fynbos	Underground storage organ	<i>Cyphia digitata</i> ; <i>Gladiolus exilis</i> ; <i>Pelargonium lobatum</i> ; <i>Pelargonium triste</i> ; <i>Rhoicissus digitata</i> ; <i>Watsonia fergusoniae</i>
	Aboveground	<i>Carissa bispinosa</i> (fruit); <i>Carpobrotus accinaciformis</i> (fruit); <i>Carpobrotus edulis</i> (fruit); <i>Cynanchum obtusifolium</i> (seedpods); <i>Euclea racemosa</i> (fruit); <i>Osyris compressa</i> (fruit); <i>Searsia glauca</i> (fruit); <i>Sideroxylon inerme</i> (fruit); <i>Tetragonia decumbens</i> (leaves); <i>Zygophyllum morganiana</i> (seed)
Sand Fynbos	Underground storage organ	<i>Gladiolus guthriei</i> ; <i>Watsonia fourcadei</i>
	Aboveground	<i>Carpobrotus edulis</i>
Strandveld	Underground storage organ	<i>Chasmanthe aethiopica</i> ; <i>Ferraria crispa</i> ; <i>Rhoicissus digitata</i>

Aboveground

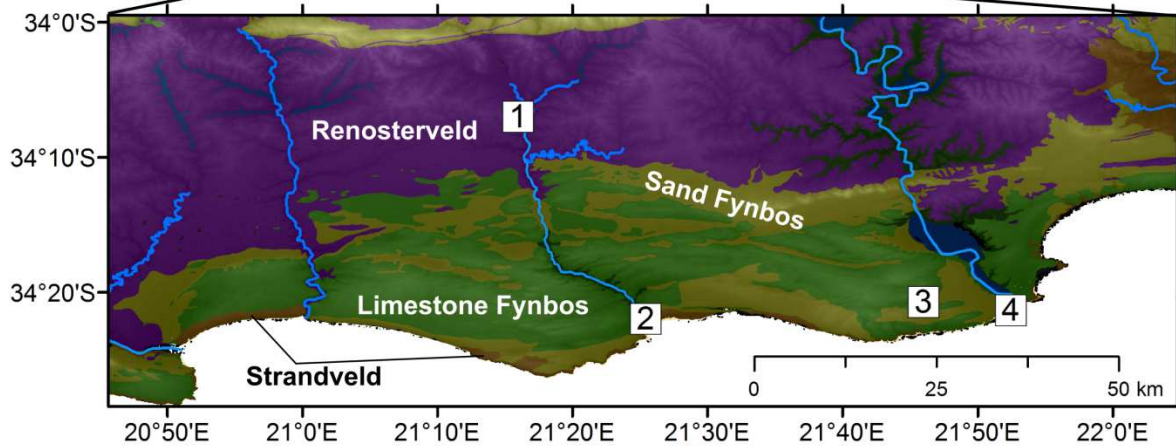
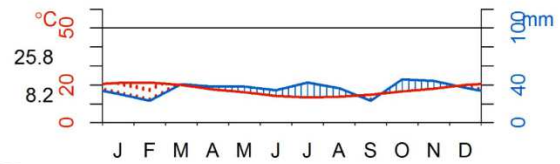
Carissa bispinosa (fruit); *Carpobrotus accinaciformis* (fruit); *Osteospermum moniliferum* (fruit); *Schotia afra* (seed); *Tetragonia decumbens* (leaves)

a)

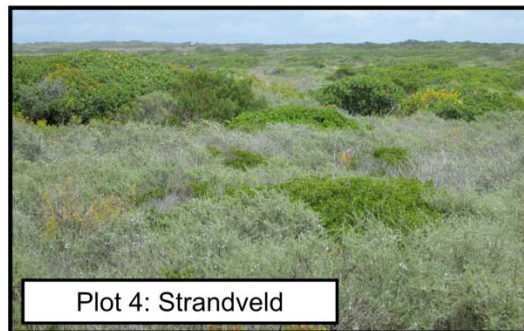
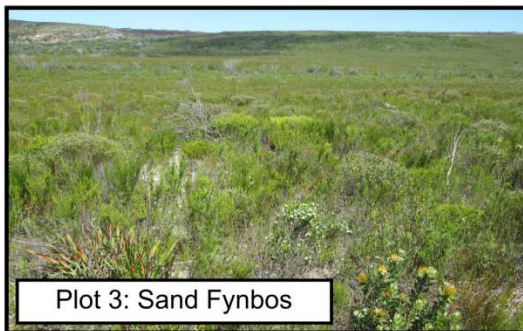
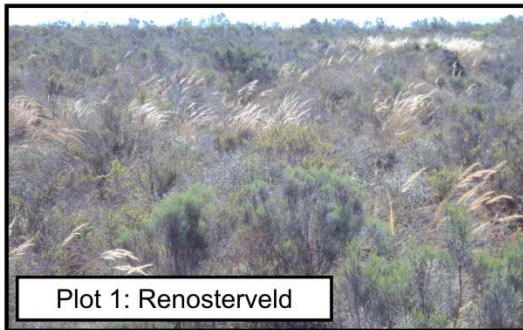


b)

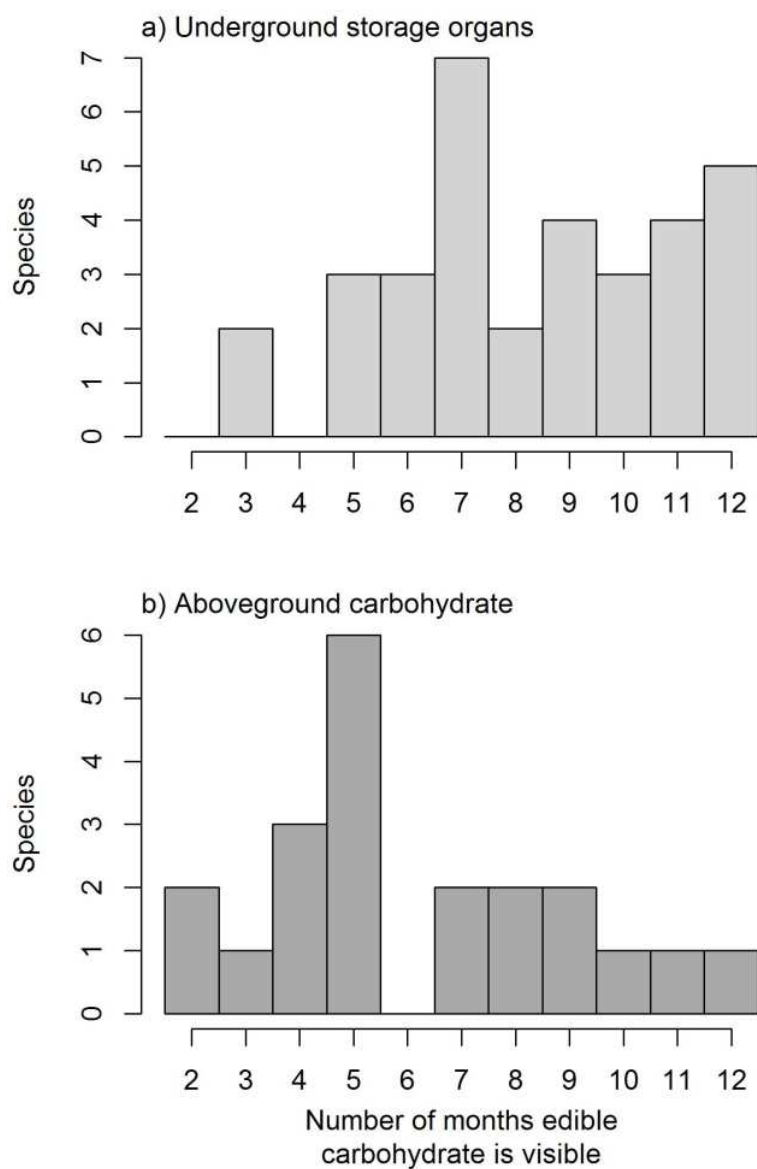
Stillbaai [0010682 0] (63 m)
1994-2014 17.2C 434 mm



c)



710 Figure 1: a) The location and major vegetation types of the study region and the plot localities [1:
711 Renosterveld (purple); 2: Limestone Fynbos (green); 3: Sand Fynbos (yellow); and 4: Strandveld
712 (orange; restricted to the coastal margin; see Tab S1 for further plot details)]. b) A Walter-Leith
713 climate diagram from the town of Still Bay (~5 km from plot 2). c) Photos taken at the four plots
714 in the different vegetation types.
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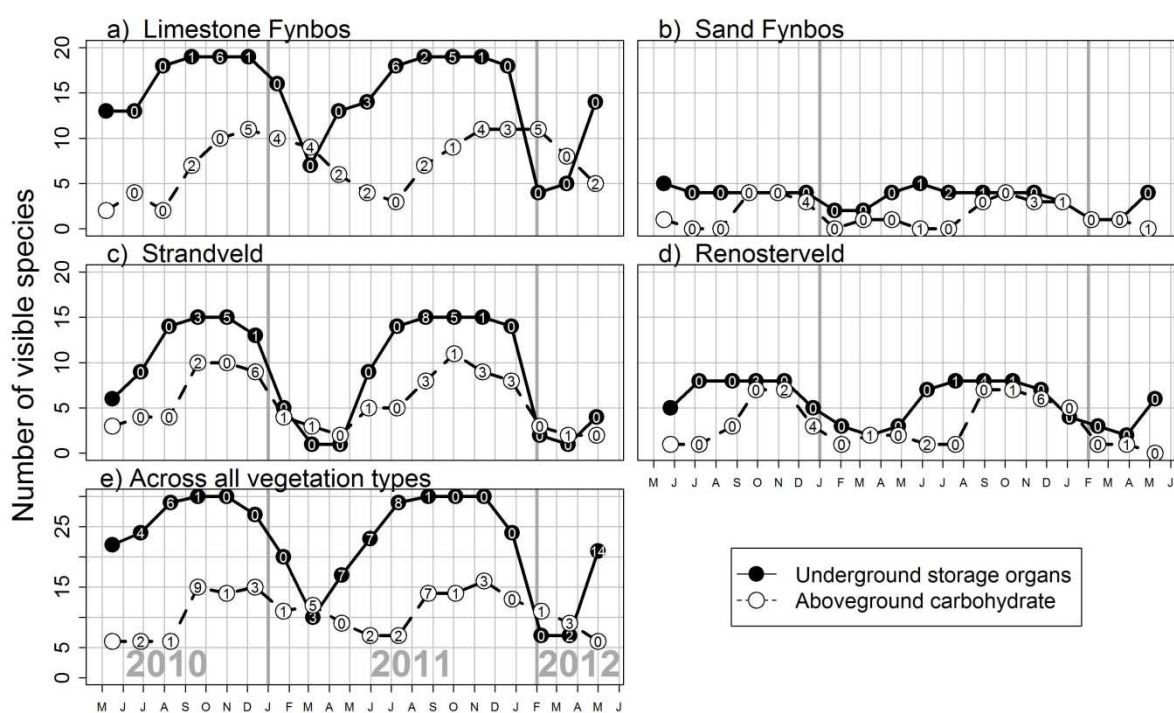


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718 Figure 2: The length of time that plant species with edible carbohydrate were available (visible)
 719 through the year, divided into a) underground storage organs (geophytes) and b) aboveground
 720 carbohydrate.

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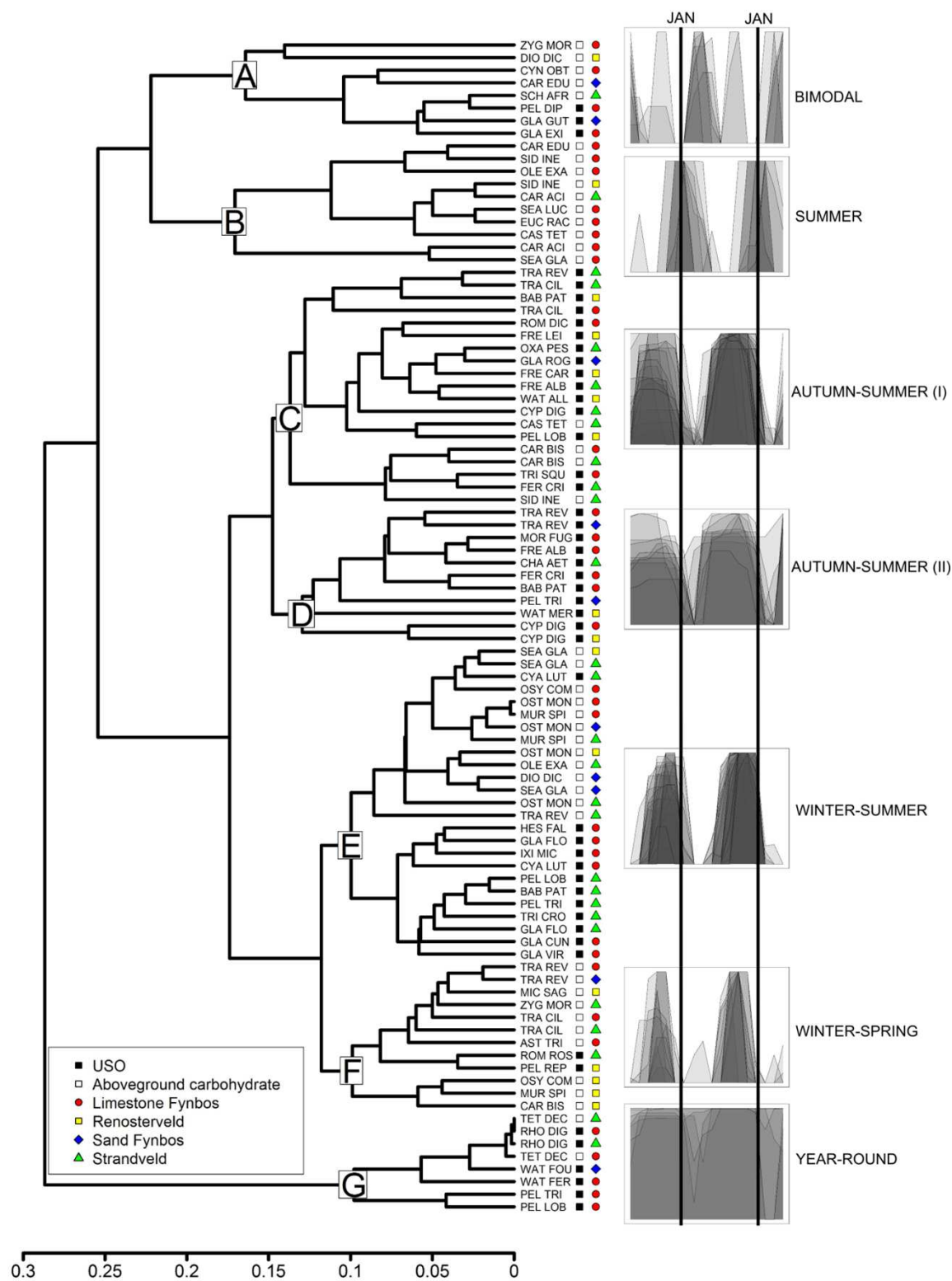


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728 Figure 3: The seasonal availability of edible species visible to a human forager in four vegetation
 729 types dominant along the Cape south coast. Underground storage organs are geophytes that have
 730 tubers, corms, bulbs or rhizomes, while above-ground carbohydrate includes species with edible
 731 fruit, seed pods, seeds, leaves or inflorescences. The number of new species observed from the
 732 previous survey is shown in each circle; this provides an indication of species turnover.

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747 Fig. 4: Dendrogram showing seven phenophases in availability of belowground (underground
748 storage organs [USOs]) and aboveground edible carbohydrates across four vegetation types
749 surveyed over two years. See Table S3.1 for explanation of the species acronyms.