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

Jan C De Vynck, Richard M Cowling, Alastair J Potts, Curtis W Marean

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.

PeerJ PrePrints | https://dx.doi.org/10.7287/peerj.preprints.1379v1 | CC-BY 4.0 Open Access | rec: 18 Sep 2015, publ: 18 Sep 2015

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

Jan C. De Vynck[1], Richard M. Cowling[1] , Alastair J. Potts[1] and Curtis W. Marean[1,2]

[1]Centre for Coastal Palaeosciences, Nelson Mandela Metropolitan University, PO Box 77 000, Port Elizabeth, 6031, Eastern Cape, South Africa

[2]Institute of Human Origins, School of Human Evolution and Social Change, PO Box 872402, Arizona State University, Tempe, Arizona 85287-2402, USA

Corresponding author:
Jan De Vynck[1]
jandevynck@vodamail.co.za

Abstract

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.

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.

PeerJ PrePrints | https://dx.doi.org/10.7287/peerj.preprints.1379v1 | CC-BY 4.0 Open Access | rec: 18 Sep 2015, publ: 18 Sep 2015

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 unpublished data), and importantly their seasonal "visibility", and thus availability, to a forager looking to initiate a foraging effort.

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

Methods

Study area

The study area is situated in the coastal plain between the Breede and Gouritz rivers on the Cape south coast (Fig. 1). The rainfall regime shows little seasonality and rain may fall at any time of the year although slight rainfall peaks are observed in March–April and with more pronounced peaks during August and October–November (Engelbrecht et al., 2014). The overall climate of the study area is semi-arid to sub-humid with annual rainfall ranging from 350 to 550 mm. The three summer months (Dec-Feb) are the most stressful for plant growth, owing to generally lower rainfall and persistently higher temperatures.

[Fig. 1 here]

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

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

Data collection

Four monitoring plots were located in representative areas of each of the major vegetation types described above: Renosterveld, Sand Fynbos, Limestone Fynbos, and Strandveld (Fig. 1). These plots were located within protected areas and were considered to be in a pristine condition. Further biophysical data for the plots are provided in Table S1. The Sand Fynbos site had burnt four years before the start of the survey period and this would likely have enhanced the visibility of USO species (Deacon, 1993), many of which flower more profusely in the early post-fire years (Le Maitre & Midgley, 1992).

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

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

Data analysis

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

We used hierarchical clustering (Anderberg, 1973) to investigate patterns of phase synchronicity (i.e. phenological timing) among edible USOs and fruiting species. Such clustering requires a dissimilarity matrix as the input. Dissimilarity was calculated as the sum of the absolute differences of relative visibility between two species (including site combinations, e.g. species 1 at site 1 versus species 1 at site 2, or species 1 at site 1 versus species 2 at site 1) for each survey date. Hierarchical clustering was performed using the *hclust* function (Pinheiro et al., 2012) and the averaging agglomeration method in R version 2.15 (R Development Core Team, 2014). Defining clusters was not performed using a strict dissimilarity threshold, but rather involved intuitive exploration of the phenograms of different potential clusters while endeavouring to maintain cluster thresholds that were fairly similar.

Results

Within the four 3.6 ha plots spread across the four vegetation types, 52 edible plant species were recorded. Of this, 33 species were geophytes with edible underground storage organs (USOs) and 21 species had aboveground edible carbohydrates (Table 1; see Table S2 for full species list per type). Note that some species had more than one edible part. Richness of edible species varied across the vegetation types (Table 1): Limestone Fynbos had the richest flora, followed by Strandveld, Renosterveld and lastly, Sand Fynbos.

[Table 1 here]

Species varied in their length of time they were available through the year (Fig. 2). Species with USOs were available for longer periods of the year relative to those with edible aboveground carbohydrates. The availability of USO species differed across vegetation types and between survey years (Fig. 3). Nonetheless, 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. In the wetter second year, the summer "crunch" period – where few USO species were available – was at least one month shorter than in the first year. The number of species with available edible aboveground carbohydrates also varied across vegetation types and sample years. Species richness peaked in spring (Sep-Nov) for all vegetation types; relatively high availability extended into summer (Dec-Feb) but autumn and early winter were lean months for harvesting aboveground carbohydrates in all vegetation types, especially Renosterveld and Sand Fynbos. The presence of two *Carpobrotus* species, which bear ripe fruits during the drier months, was a key factor for the extension of aboveground availability period in Limestone Fynbos.

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

[Fig. 2 here]

[Fig. 3 here]

[Table 2 here]

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

[Fig. 4 here]

Discussion

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

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

Late summer to early autumn have considerably fewer available edible species than in the other times of the year. This is a period when all traces of leaves and inflorescences of the dominant deciduous geophyte component have disappeared (Deacon, 1993). However, even during this relatively warm and dry period, we recorded some 25 available species across the four vegetation types (Table 2). These include USOs such as hysteranthous, autumn-flowering *Gladiolus* (cormous) and *Pelargonium* (tuberous) spp, the corms of evergreen *Watsonia* spp., and the fibrous tubers of the evergreen liana, *Rhoicissus digitata.* Also apparent are the fruits *Carpobrotus* spp, the fruits of many subtropical shrubs and trees, and the leaf crop, *Tetragonia decumbens.* Nonetheless, the late summer – early autumn months could represent a carbohydrate "crunch" for foragers: at this time the number of edible plant species is at its lowest and the high-biomass items available to foragers (e.g. *Pelargonium* spp., *R. digitata*) are fibrous and require cooking for digestion (Deacon, 1995; Dominy et al., 2008).

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

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

Given the temporal and spatial availability of edible plant species in the Cape, we argue that is highly likely that USOs, fruit, seedpods, seeds, inflorescences and leaf crops were harvested as fallback foods by Stone Age people living in this region. The preferred food for south Cape coastal hunter-gatherers comprised the region's diverse and abundant marine resources (Marean et al., 2007; Jerardino & Marean, 2010; Parkington, 2010), and a diverse ungulate plains fauna, including in the Pleistocene, several species of now extinct megafauna, associated with the submerged Agulhas Bank (Klein, 1983; Parkington, 2001, 2003; Matthews, Marean & Nilssen, 2009; Marean, 2010; Faith, 2011). However, these resources were not always available to harvesters and hunters, and the contraction and expansion of the Agulhas Plain ecosystem and its ungulate communities must have been a major driver of changing foraging patterns on the south coast (Marean et al., 2014). It has been hypothesized that the mammal fauna formed a migratory community that moved west during the winter rains and east to intercept the summer rains. Thus, the local abundance of many of the larger ungulates may have plummeted during the winter months when populations migrated west to graze winter-growing grasses of the west coast. Marine invertebrates, harvested from the intertidal, comprised the most reliable and accessible source of protein for hunter-gatherers living on the Cape south coast (Marean, 2011). Evidence for their use has been found in MSA sites such as Pinnacle Point (PP) 13B dating back to ~160 ka (Marean et al., 2007; Jerardino & Marean, 2010) and at early modern human sites that date between 110-50 ka such as Blombos Cave (Henshilwood et al., 2001; Langejans et al., 2012), and Klasies River Mouth (Voigt, 1973; Thackeray, 1988). Late Stone Age sites suggest an increase in the intensity of intertidal foraging (Marean et al., 2014) and indications of resource depletion (Klein & Steele, 2013). Using experienced foragers of Khoe-San descent, J. De Vynck et al. (unpublished data) showed exceptionally high peak return rates (~4,500 kcal hr^{-1}) from the Cape south coast intertidal under ideal harvesting conditions. However, owing to tidal constraints, and the fierce sea conditions experienced there, harvesting was only possible for 10 days a month, for 2-3 hours on each day; lowest returns were recorded in winter and spring – a time of strong winds and high seas – and highest returns in summer and autumn, when sea conditions were calmer (J. De Vynck et al., unpublished data). Consequently, there would have been periods of various lengths – ranging from days to weeks – when hunter-gatherers depended on, or fell back upon carbohydrates for sustenance. As pointed out above, the winter and early spring months likely coincided with a scarcity of protein but an abundance of carbohydrates. At these times, plant carbohydrates, especially USOs, may have comprised 100% of dietary intake, which would categorise them as a staple fallback food (Marshall & Wrangham, 2007).

It has been hypothesized that the persistence of a small group of hominins on the Cape south coast – as opposed to their widespread extinction elsewhere in Africa during Marine Isotope Stage 6 (MIS6, 193 000 -125 000 BP) (Foley, 1998; Lahr & Foley, 1998; Fagundes et al., 2007;

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

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

Acknowledgements

We thank the Cape Nature team - Rhett Heismann, Jean Du Plessis and Leandi Wessels - for access, support, information and GIS assistance. We also thank the Hessequa Municipality, and in particular Hendrik Visser, for their help and support.

The South African Weather Service, Chris Pentz and Mr. Fransen supplied climate data and is much appreciated.

References

Abanda PA, Compton JS, Hannigan RE. 2011. Soil nutrient content, above-ground biomass and litter in a semi-arid shrubland, South Africa. *Geoderma* 164 (3-4): 128-137.

Anderberg MR. 1973. *Cluster analysis for applications* (No. OAS-TR-73-9). New Mexico: Office of the Assistent for Study Support Kirtland AFB.

Basell LS. 2008. Middle Stone Age (MSA) site distributions in eastern Africa and their relationship to Quaternary environmental change, refugia and the evolution of Homo sapiens. *Quaternary Science Reviews* 27 (27): 2484-2498.

Bergh NG, Verboom GA, Rouget M, Cowling RM. 2014. Vegetation types of the Greater Cape Floristic Region. In: Allsopp N, Colville JF, Verboom T, eds. *Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region.* , Oxford: Oxford University Press, 1-25.

Berbesque JC, Marlowe FW. 2009. Sex differences in food preferences of Hadza Hunter-Gatherers. *Evolutionary Psychology* 7 (4): 601-616.

Bird DW, Bliege Bird RB, Parker CH. 2005. Aboriginal burning regimes and hunting strategies in Australia's Western Desert. *Human ecology* 33 (4): 443-464.

Bleek WHI, Lloyd LC. 1911. *Specimens of Bushmen folklore*. London: George Alan and Company.

Bliege Bird RB, Bird DW, Codding BF, Parker CH, Jones JH. 2008. The "fire stick farming" hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proceedings of the National Academy of Sciences* 105: 14796-14801.

Cawthra HC, Compton JS, Fisher EC, MacHutchon MR, Marean CW. 2015. Submerged shorelines and landscape features offshore of Mossel Bay, South Africa. *Geological Society, London, Special Publications* 411: SP411-11.

Cowling RM. 1990. Diversity components in a species-rich area of the Cape Floristic Region. *Journal of Vegetation. Science* 1: 699-710.

Cowling RM, Lombard AT. 2002. Heterogeneity, speciation/extinction history and climate: explaining regional plant diversity patterns in the Cape Floristic Region. *Diversity and Distributions* 8 (3): 163-179.

Cowling RM, Kirkwood D, Midgley JJ, Pierce SM 1997. Invasion and persistence of bird-dispersed, subtropical thicket and forest species in fire-prone fynbos. Journal of Vegetation *Science* 8: 475-488.

Deacon HJ. 1970. Plant remains from Melkhoutboom Cave, South Africa. *Proceedings Transkei and Ciskei Research Society* 1: 13-15.

Deacon HJ. 1976. *Where hunters gathered: a study of Holocene Stone Age people in the Eastern Cape*. Claremont: South African Archaeological Society.

Deacon HJ. 1979. Excavations at Boomplaas cave-a sequence through the upper Pleistocene and Holocene in South Africa. *World Archaeology* 10 (3): 241-257.

Deacon HJ. 1993. Planting an Idea: An Archaeology of Stone Age Gatherers in South Africa. *The South African Archaeological Bulletin* 48: 86-93.

Deacon HJ. 1995. Two late Pleistocene-Holocene archaeological depositories from the southern Cape, South Africa. *The South African Archaeological Bulletin* 121-131.

Deacon J. 1984. Later Stone Age people and their descendants in southern Africa. In: Klein RG ed. *Southern African prehistoric and paleoenvironments*. Rotterdam/Boston: A. A. Balkema, 220-328.

Deacon HJ, Deacon J. 1963. Scott's Cave: a late Stone Age site in the Gamtoos Valley Annals of the Cape Provincial Museums. *Natural History* 3: 96-112.

Deacon HJ, Deacon J. 1999. *Human beginnings in South Africa: Uncovering the secrets of the Stone Age.* Cape Town: David Philip Publishers (Pty) Ltd.

De Vynck JC, Van Wyk BE, Cowling RM. 2015. Indigenous Edible Plant Use by Contemporary Khoe-San Descendants of South Africa's Cape South Coast. *South African Journal of Botany,* in press.

Dominy NJ, Vogel ER, Yeakel JD, Constantino P, Lucas PW. 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early Hominins. *Evolutionary Biology* 35: 159–175.

Engelbrecht CJ, Landman WA, Engelbrecht FA, Malherbe J. 2014. A synoptic decomposition of rainfall over the Cape south coast of South Africa. *Climate Dynamics* 44 (9-10): 2589-2607.

Fagundes NJ, Ray N, Beaumont M, Neuenschwander S, Salzano FM, Bonatto SL, Excoffier L. 2007. Statistical evaluation of alternative models of human evolution. *Proceedings of the National Academy of Sciences* 104 (45): 17614-17619.

Faith JT. 2011. Ungulate community richness, grazer extinctions, and human subsistence behavior in southern Africa's Cape Floral Region. *Palaeogeography, Palaeoclimatology, Palaeoecology* 306 (3): 219-227.

Fisher EC, Bar-Matthews MJA, Marean CW. 2010. Middle and Late Pleistocene paleoscape modeling along the southern coast of South Africa. *Quaternary Science Reviews* 29 (11): 1382-1398.

Foley R. 1998. The context of human genetic evolution. *Genome Research* 8 (4): 339-347.

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

Hatley T, Kappelman J. 1980. Bears, pigs, and plio-Pleistocene Hominids: A case for the exploitation of belowground food resources. *Human Evolution* 8: 371-387.

Henshilwood CS, Sealy JC, Yates R, Cruz-Uribe K, Goldberg P, Grine FE, Klein RG, Poggenpoel C, van Niekerk K, Watts I. 2001. Blombos Cave, southern Cape, South Africa: preliminary report on the 1992–1999 excavations of the Middle Stone Age levels. *Journal of Archaeological Science* 28 (4): 421-448.

Jerardino A, Marean CW. 2010. Shellfish gathering, marine paleoecology and modern human behavior: perspectives from cave PP13B, Pinnacle Point, South Africa. *Journal of Human Evolution* 59 (3-4): 412-424.

Kaye B, Moodie DW. 1978. The Psoralea food resource of the Northern Plains. *Plains Anthropologist* 23: 329-36

Klein RG. 1983. Palaeoenvironmental implications of Quaternary large mammals in the fynbos region. In: Deacon HJ, Hendey QB, Lambrechts JJN, eds. *Fynbos paleoecology: a preliminary synthesis.* Pretoria: South African National Scientific Programmes Report, 75: 116-138.

Klein RG, Steele TE. 2013. Archaeological shellfish size and later human evolution in Africa. *Proceedings of the National Academy of Science* 110 (27): 10910-10915.

Kyriacou K, Parkington JE, Marais AD, Braun DR. 2014. Nutrition, modernity and the archaeological record: Coastal resources and nutrition among Middle Stone Age hunter-gatherers on the western Cape coast of South Africa. *Journal of Human Evolution* 77: 64-73.

Lahr MM, Foley RA. 1998. Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. *Yearbook of physical anthropology*, 41: 137-176.

Langejans GHJ, van Niekerk KL, Dusseldorp GL, Thackeray JF. 2012. Middle Stone Age shellfish exploitation: Potential indications for mass collecting and resource intensification at Blombos Cave and Klasies River, South Africa. *Quaternary International* 270: 80-94.

Lee RB. 1969. !Kung Bushman subsistence: An input-output analysis. In: Vayda AP, ed. *Environment and cultural behaviour*. Austin: University of Texas Press, 47-79.

Lee RB. 1973. Mongongo: The ethnography of a major wild food resource. *Ecology of Food and Nutrition* 2 (4): 213-307.

Lee RB. 1984. *The Dobe !Kung*. New York: Holt, Rinehart and Winston, Inc., 40-44.

Le Maitre DC, Midgley JJ. 1992. Plant reproductive ecology. In: Cowling RM, ed. *The ecology of Fynbos: nutrients, fire and diversity*. Cape Town: Oxford University Press, 135-174.

Liengme C. 1987. Botanical remains from archaeological sites in the Western Cape. *Paper in the prehistory of the Western Cape.* Oxford: BAR International Series, 237-261.

Malan JA. 1987. The Bredasdorp Group in the area between Gans Bay and Mossel Bay. *South African Journal of Science* 83 (8): 506-507.

Marean CW. 2010. Pinnacle Point Cave 13B (Western Cape Province, South Africa) in context: the Cape Floral kingdom, shellfish, and modern human origins. *Journal of Human Evolution* 59 (3-4): 425-443.

Marean CW. 2011. Coastal South Africa and the coevolution of the modern human lineage and the coastal adaptation. In: Bicho NS, Haws JA, Davis LG, eds. *Trekking the shore. Interdisciplinary contributions to Archaeology.* New York: Springer, 421-440.

Marean CW, Bar-Matthews M, Bernatchez J, Fisher E, Goldberg P, Herries AIR, Jacobs Z, Jerardino A, Karkanas P, Minichillo T, Nilssen PJ, Thompson E, Watts I, Williams HM. 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* 449 (7164): 905-908.

Marean CW, Cawthra HC, Cowling, RM, Esler KJ, Fisher E, Milewski A, Potts AJ, De Vynck JC. 2014. Stone Age People in a Changing South African Greater Cape Floristic Region. In:

Allsopp N, Colville JF, Verboom T, eds. *Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region.* Oxford: Oxford University Press, 164-199.

Marean CW, Anderson RJ, Bar-Matthews M, Braun K, Cawthra HC, Cowling RM, Engelbrecht F, Esler KJ, Fisher E, Franklin J, Hill K, Janssen M, Potts AJ, Zahn R. 2015. A new research strategy for integrating studies of paleoclimate, paleoenvironment, and paleoanthropology. *Evolutionary Anthropology: Issues, News, and Reviews* 24 (2): 62-72.

Marshall A, Wrangham R. 2007. Evolutionary consequences of fallback foods. *International Journal of Primatology* 28: 1219-1235.

Marlowe FW, Berbesque JC. 2009. Tubers as fallback foods and their impact on Hadza Hunter-Gatherers. *American Journal of Physical Anthropology* 140 (4): 751-758.

Masson-Delmotte V, Stenni B, Pol K, Braconnot P, Cattani O, Falourd S, Kageyama M, Jouzel J, Landais A, MinsterB, Barnola JM, Chappellaz J, Krinner G, Johnsen S, Rothlisberger R, Hansen J, Mikolajewicz U, Otto-Bliesner B. 2010. EPICA Dome C record of glacial and interglacial intensities. *Quaternary Science Reviews* 29(1): 113-128.

Matthews T, Marean CW, Nilssen, PJ. 2009. Micromammals from the Middle Stone Age (92 000 – 167 000 ka) at Cave PP13B, Pinnacle Point, south coast, South Africa. *Paleontologia Africana* 4: 112-120.

Murray SS, Schoeninger MJ, Bunn HT, Pickering TR, Marlett, J. A. 2001. Nutritional Composition of Some Wild Plant Foods and Honey Used by Hadza Foragers of Tanzania. *Journal of Food Composition and Analysis* 14: 3-13.

Negre C, Zahn R, Thomas AL, Masqué P, Henderson GM, Martínez-Méndez G, Hall IR, Mas JL. 2010. Reversed flow of Atlantic deep water during the Last Glacial Maximum. *Nature* 468 (7320): 84-88.

Opperman H, Heydenrych B. 1990. A 22 000 Year-Old Middle Stone Age camp site with plant food remains from the North-Eastern Cape. *The South African Archaeological Bulletin* 45 (152): 93-99.

Parkington JE. 1977. Soaqua: Hunter-fisher-gatherers of the Olifants River valley Western Cape. *South African Archaeological Society* 32: 150-157.

Parkington JE. 2001. Milestones: the impact of the systematic exploitation of marine foods on human evolution. In: Tobias PV, Raath MA, Moggi-Cecci J, Doyle GA, eds. *Humanity from African naissance to coming Millennia - colloquia in human biology and palaeoanthropology.* Firenze: Firenze University Press, 327-336.

Parkington J. 2003. Middens and moderns: shellfishing and the Middle Stone Age of the Western Cape, South Africa. *South African Journal of Science* 99 (5/6): 243.

Parkington J. 2006. Shorelines, strandlopers and shell middens: Archaeology of the Cape Coast. Cape Town: Krakadouw.

Parkington J. 2010. Coastal diet, encephalization, and innovative behaviors in the late Middle Stone Age of southern Africa. *Human Brain Evolution: The Influence of Freshwater and Marine Food Resources.* New York: Wiley-Blackwell, 189-202.

Parkington JE, Poggenpoel C. 1971. Excavations at de Hangen, 1968. *The South African Archaeological Bulletin* 26: 3-26.

Pierce SM. 1984. *A synthesis of plant phenology in the Fynbos Biome*. South African National Scientific Programmes Report no. 88. Pretoria: Graphics art division of the CSIR, 29.

Pinheiro J, Bates D, DebRoy S, Sarkar D. 2012. R Development Core Team. nlme: Linear and nonlinear mixed effects models, 2012. *URL http://CRAN. R-project. org/package= nlme. R package version*, 3-1.

Procheş S, Cowling RM, du Preez DR. 2005. Patterns of geophyte diversity and storage organ size in the winter-rainfall region of southern Africa. *Diversity and Distributions* 11 (1): 101-109.

Procheş S, Cowling RM, Goldblatt P, Manning JC, Snijman DA. 2006. An overview of the Cape geophytes. *Biological Journal of the Linnean Society* 87 (1): 27-43.

R Development Core Team. 2014. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical computing, ISBN 3-900051-07-0, URL http://www.R-project.org

Rebelo AG, Cowling RM, Campbell BM, Meadows M. 1991. Plant communities of the Riversdale plain. *South African Journal of Botany* 57: 10-28.

Rogers J. 1984. *Cenozoic geology of the southern Cape coastal plain between Cape Agulhas and Mossel Bay, focussing on the area between the Kafferkuils and Gouritz rivers*. Technical report No. 15: University of Cape Town: Marine Geoscience Unit.

Ruiters C, McKenzie B. 1994. Seasonal allocation and efficiency patterns of biomass and resources in the perennial geophyte Sparaxis grandiflora subspecies fimbriata (Iridaceae) in lowland coastal fynbos, South Africa. *Annals of Botany* 74 (6): 633-646.

Schwegler M. 2003. *Medicinal and Other Uses of Southern Overberg Fynbos Plants*. Cape Town: M. Schwegler.

Skead CJ, Manning JC, Anthony NC. 2009. *Historical plant incidence in southern Africa: a collection of early travel records in southern Africa*. Pretoria: South African National Biodiversity Institute.

Thackeray JF. 1988. Molluscan Fauna from Klasies River, South Africa. *South African Archaeological Bulletin* 43: 27-32.

Thwaites RN, Cowling RM. 1988. Soil-vegetation relationships on the Agulhas plain, South Africa. *Catena* 15 (3): 33345.

Van Vuuren H. 2014. 'A song sung by the star !Gaunu, and especially by Bushman women': the blossoming of the uintjieblom. In: Deacon J, Skotnes P. *The courage of //kaboo. Celebrating the 100th anniversary of the publication of* Specimens of Bushman Folklore. Cape Town: UCT Press, 317-328.

Van Wyk BE. 2002. A review of ethnobotanical research in South Africa. *South African Journal of Botany* 68: 1–13.

Van Wyk BE, Gericke N. 2000. *People's plants: a guide to useful plants of southern Africa*. Johannesburg: Briza Publications.

Vincent AS. 1985. *Underground Plant Foods and Subsistence in Human Evolution*. California: University of California at Berkeley.

Voigt E, 1973. Klasies River Mouth Cave: An exercise in shell analysis. *Bulletin of the Transvaal Museum* 14: 14-15.

Wells MJ. 1965. An analysis of plant remains from Scott's Cave in the Gamtoos Valley. *The South African Archaeological Bulletin* 79-84.

Willis CK, Lombard AT, Cowling RM, Heydenrych BJ, Burgers CJ. 1996. Reserve systems for limestone endemic flora of the Cape lowland fynbos: iterative versus linear programming. *Biological Conservation* 77 (1): 53-62.

Zahn R, Lutjeharms J, Biastoch A, Hall I, Knorr G, Park W, Reason C. 2010. Investigating the global impacts of the Agulhas Current. *Eos, Transactions American Geophysical Union* 91 (12): 109-110.

Table 1: Summary of edible species in 3.6 ha plots situated in four dominant vegetation types 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

[1] 'Other' includes species with edible: seed pods, seeds, leaves, and inflorescences.
[2] Note that this is the number of unique species (i.e. some species are shared between vegetation types or have more than one edible part).

Table 2: Species available during the 'carbohydrate-crunch' late summer period (February-March) in both survey years.

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

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

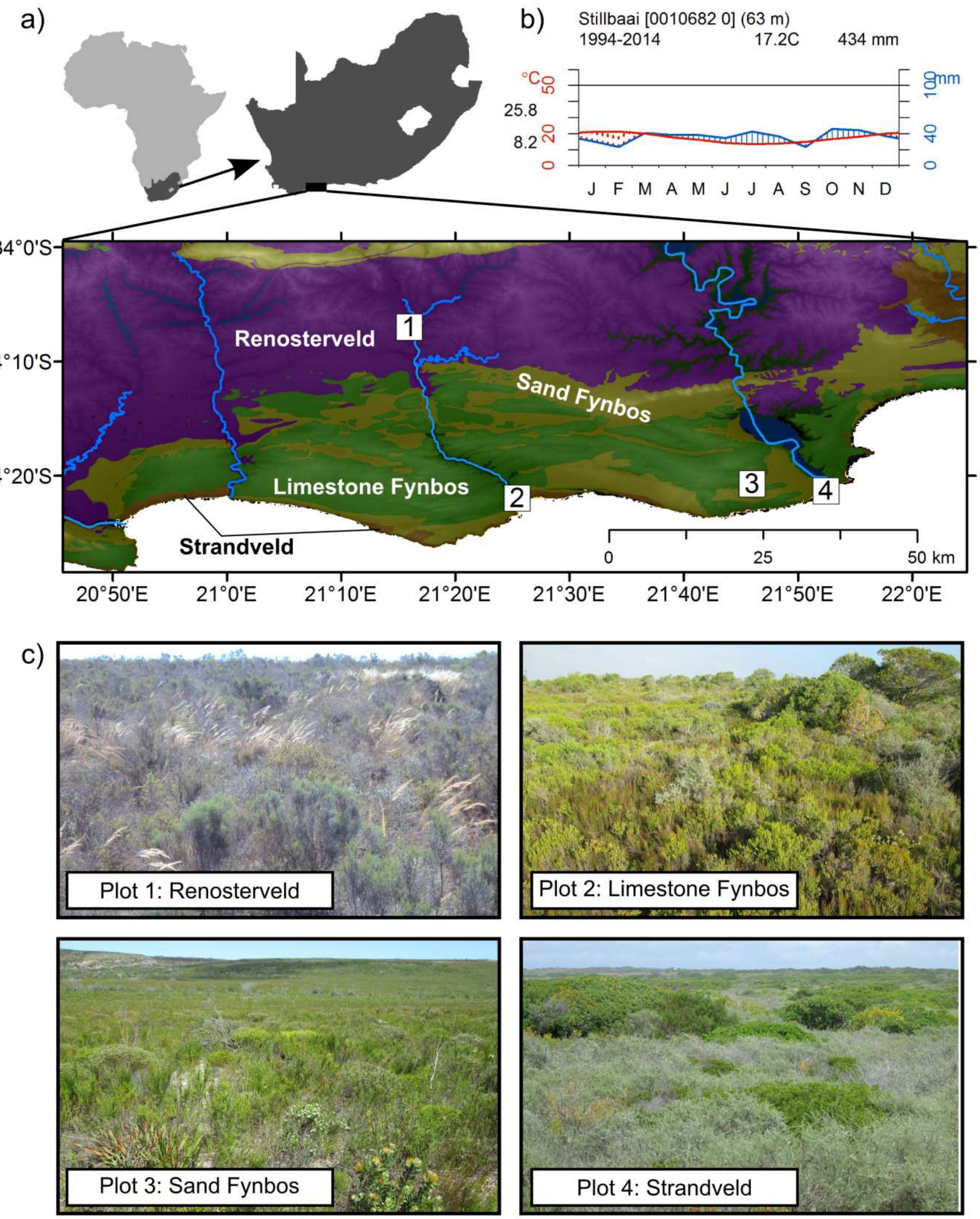


Figure 1: a) The location and major vegetation types of the study region and the plot localities [1: Renosterveld (purple); 2: Limestone Fynbos (green); 3: Sand Fynbos (yellow); and 4: Strandveld (orange; restricted to the coastal margin; see Tabe S1 for further plot details)]. b) A Walter-Leith climate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

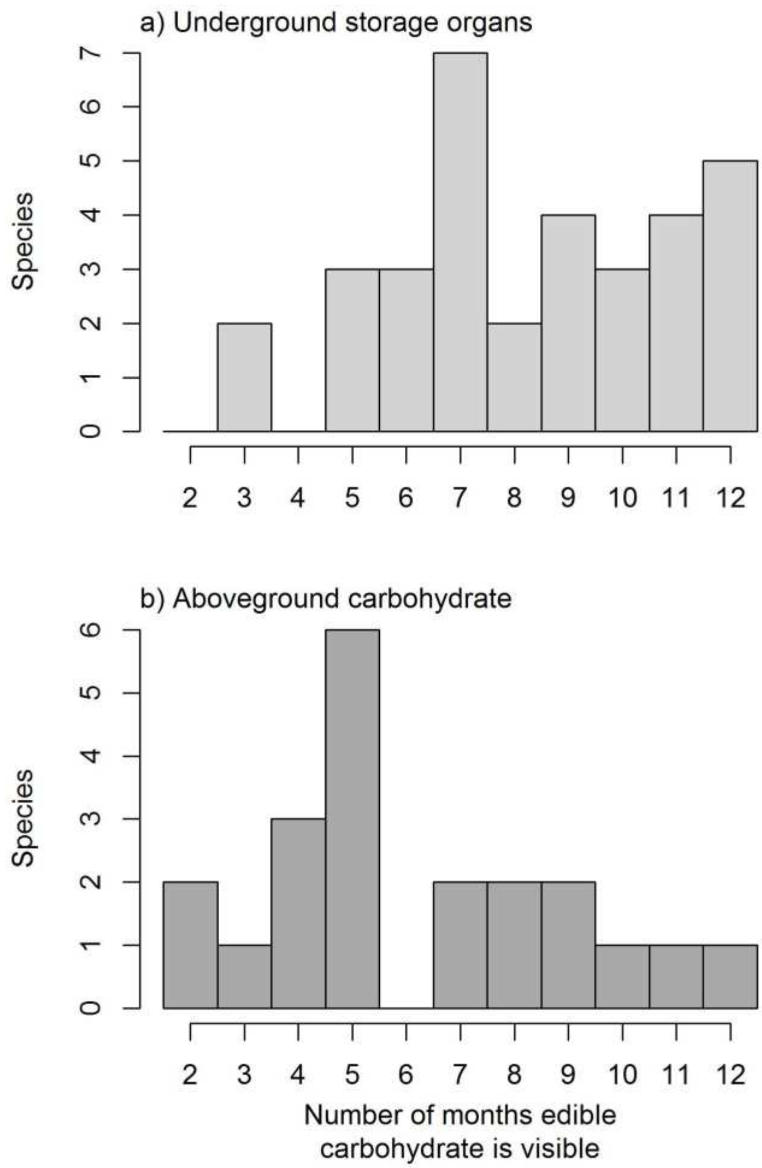


Figure 2: The length of time that plant species with edible carbohydrate were available (visible) through the year, divided into a) underground storage organs (geophytes) and b) aboveground carbohydrate.

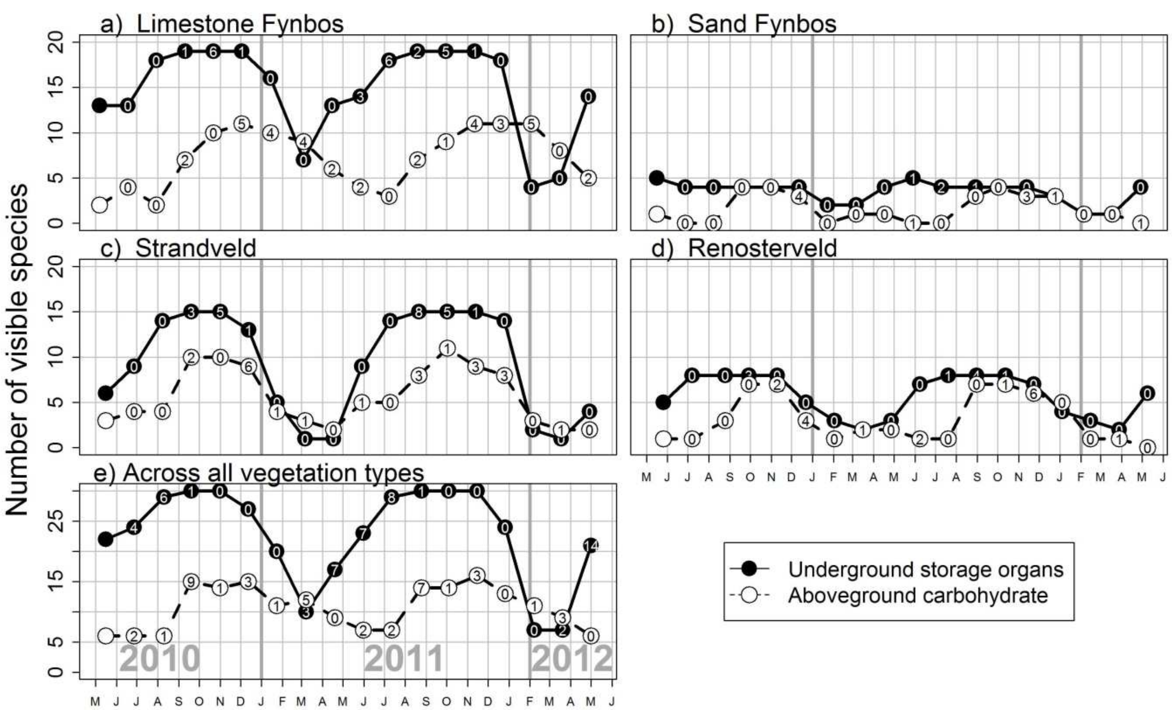
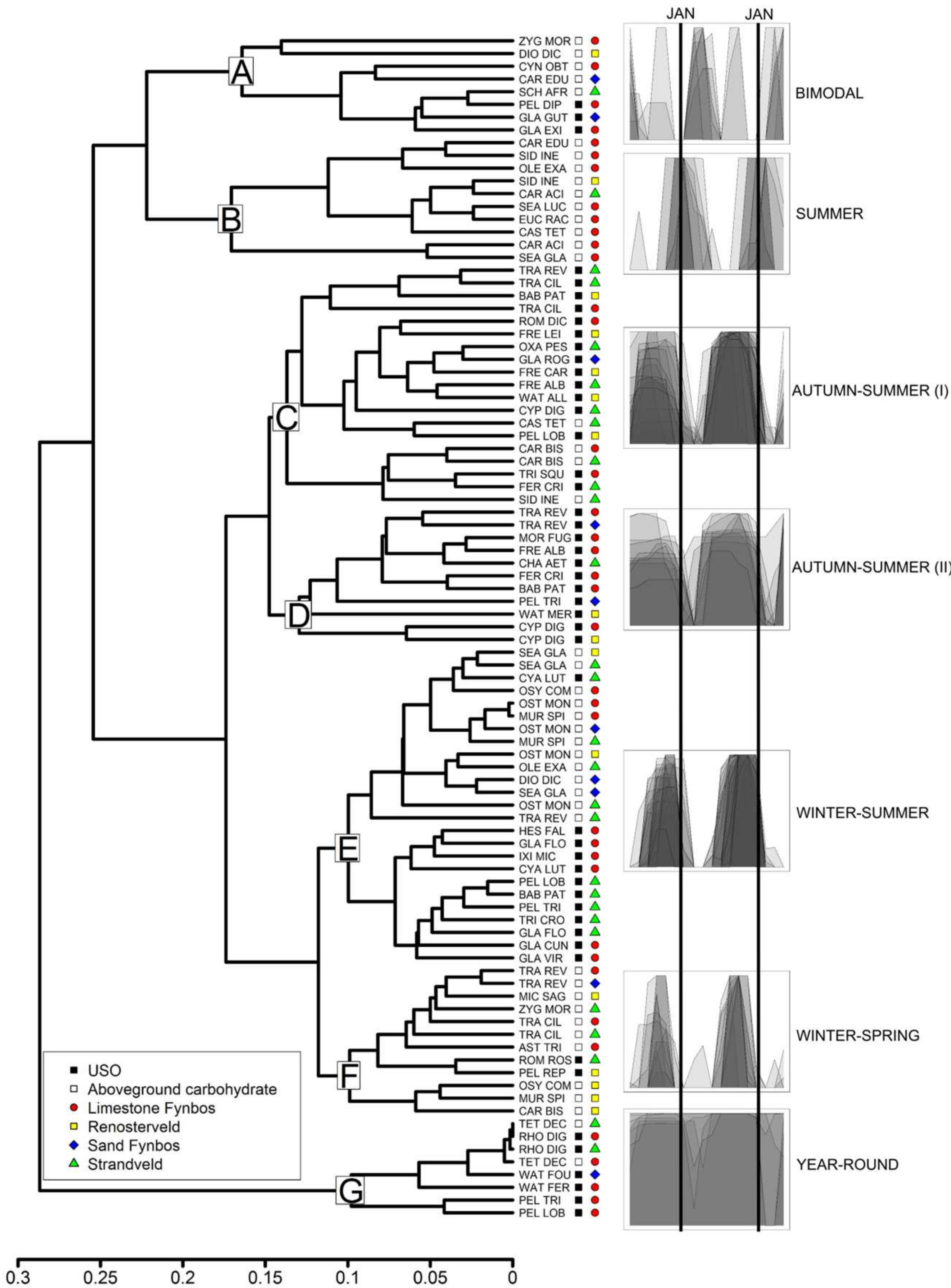


Figure 3: The seasonal availability of edible species visible to a human forager in four vegetation types dominant along the Cape south coast. Underground storage organs are geophytes that have tubers, corms, bulbs or rhizomes, while above-ground carbohydrate includes specie with edible fruit, seed pods,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


JAN
JAN
A
B
C
D
E
F
G
BIMODAL
SUMMER
AUTUMN-SUMMER (I)
AUTUMN-SUMMER (II)
WINTER-SUMMER
WINTER-SPRING
YEAR-ROUND
USO
Aboveground carbohydrate
Limestone Fynbos
Renosterveld
Sand Fynbos
Strandveld
0.3
0.25
0.2
0.15
0.1
0.05
0

745

746

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