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The Palaeo-Agulhas Plain: Temporal and spatial variation in an extraordinary extinct ecosystem of the Pleistocene of the Cape Floristic Region

Curtis W. Marean [a, c, *], Richard M. Cowling [a], Janet Franklin [a, b]

[a] *African Centre for Coastal Palaeoscience, Botany Department, Nelson Mandela University, PO Box 77000, Port Elizabeth, 6031, South Africa*
[b] *Department of Botany and Plant Sciences, University of California – Riverside, 900 University Ave, Riverside, CA, 92521, USA*
[c] *Institute of Human Origins, School of Human Evolution and Social Change, PO Box 872402, Arizona State University, Tempe, AZ, 85287-2402, USA*

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ABSTRACT

At the height of its extent, during strong glacials, the Palaeo-Agulhas Plain (PAP, south coast of South Africa) was the size of Ireland, sometimes doubling the size of the extant Cape Floristic Region (CFR). During strong interglacial climates, the PAP was mostly submerged and its ecosystems destroyed or restricted to small slivers. Scientists have largely ignored the PAP, presumably because it is submerged. We argue the PAP contributed to the diversification of the mega-diverse CFR biota and was the most productive foraging habitat available to the early modern humans that inhabited the famous archaeological sites along the current coast. We synthesize the palaeo-archival evidence and modeling results from this special issue, and other results, and propose a general model for the Last Glacial Maximum PAP, and offer suggestions as to conditions during marine isotope stages (MIS) 6 and 4. Unlike the region today, the PAP included abundant nutritious grassland, savanna-like floodplains, numerous wetlands, and a soft and highly dynamic coastline. Grasslands dominated the northern plains and fynbos shrublands the southern plains, both cut by broad meandering rivers with extensive floodplain woodlands and grasslands. The high productivity of the northern sector PAP supported a diverse plains fauna and rich habitats for humans living along its northern fringe, and during MIS 4 they had access to large ungulates on the grasslands, coastal resources, and plant foods from the plain and interior. The Holocene and historical contact period provide our current model of human and ecological conditions in the CFR region, but should be interpreted as a low-resource outlier.

1. Introduction

The Cape Floristic Region (CFR), a relatively small region on a global scale (Allsopp et al., 2014), garners an enormous amount of scientific interest. It contains a mega-diverse and unique flora that has been a continual focus of fascination and study. Concentrated on its current shore are a large sample of caves and rock shelters that contain world-renowned palaeo-archives of early modern human biology, behavior, and culture (Marean et al., 2014; Wadley, 2015). These same caves and rockshelters, along with some open-air localities, preserve extensive records of faunal change that document extraordinary shifts in faunal communities, communities that seem to change more dramatically since the onset of the Holocene than anywhere else in Africa (Klein, 1983). Its oceanic peculiarities, shaped by colliding cold upwelling and warm tropical currents, create a rich two-ocean environment (Branch and Menge, 2001) of intense interest to the public and marine scientists. In addition, its geology preserves rich palaeoarchives that have cultivated a long and distinguished record of Quaternary science.

Despite this ardent scientific gaze, there is a cryptic but crucial feature of the CFR's character that has remained largely underappreciated and understudied, sometimes forgotten. Scientists have known for half a century that a submerged landscape, most widely expressed on the central southern shores of the CFR (Fig. 1), existed underwater (Dingle, 1970a, b; Slater, 1970). This knowledge failed to translate into appreciation of the potential significance of this

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[*] Corresponding author. Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, PO Box 872402, Tempe, AZ, 85287-2402, USA.
E-mail addresses: curtis.marean@asu.edu (C.W. Marean), rmcowling27@gmail.com (R.M. Cowling), janet.franklin@ucr.edu (J. Franklin).

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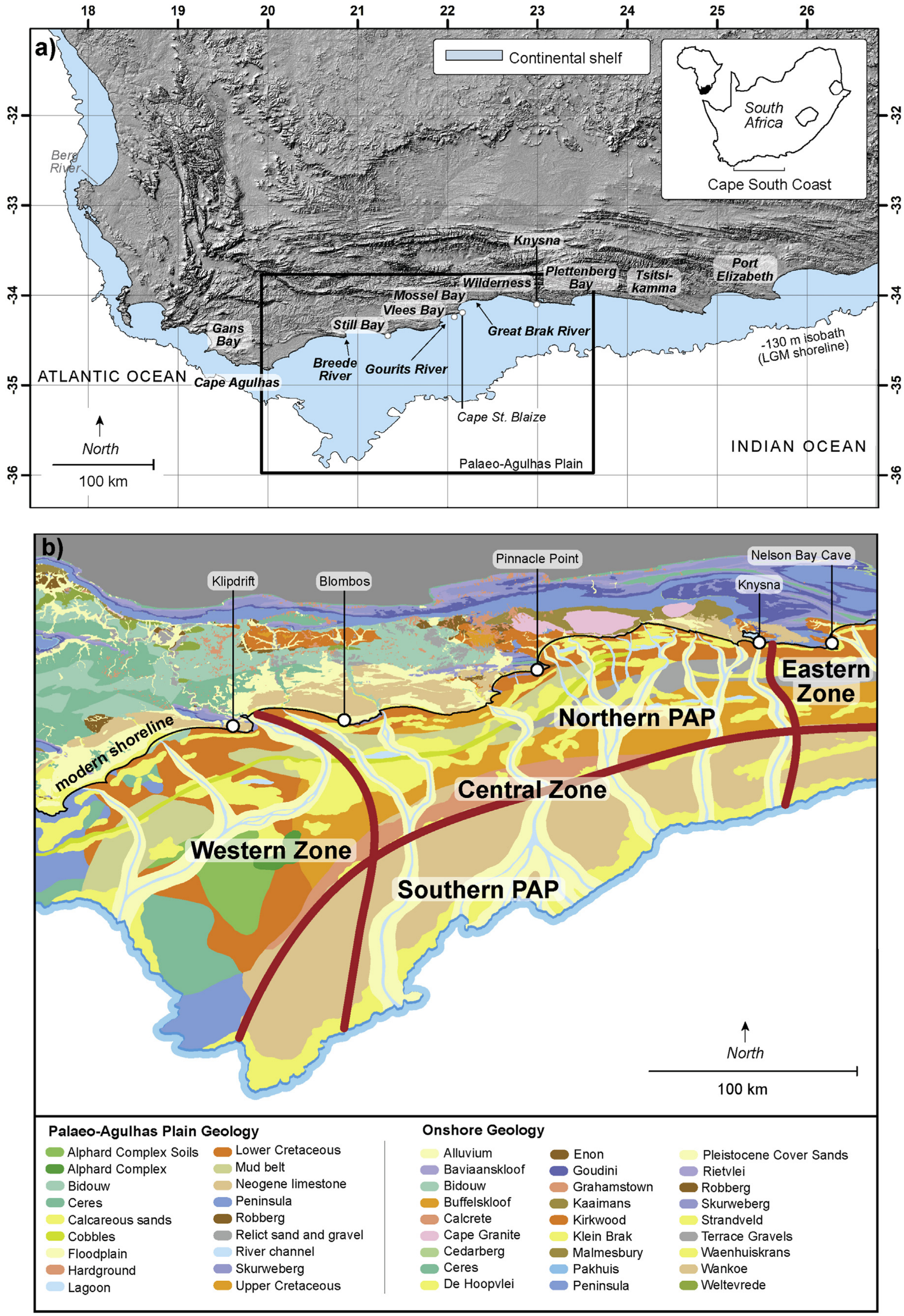

Fig. 1. Maps of the Palaeo-Agulhas Plain. a) Southern-most Africa with the maximum extent of the continental shelf shown, and the inset shows our focal area of study within the Palaeo-Agulhas Plain. (Source: Cawthra et al., 2020b [this issue]). b) A geological map of the Cape Floristic Region and the Palaeo-Agulhas Plain from Cawthra et al., (2020b [this issue]), redrawn for this paper by Patrick Fahey, showing our defined zones, and several sites that have provided important human and palaeo-archival records.

ancient ecosystem for virtually all of those things that have drawn that selfsame scientific fascination – floral diversity, massive faunal change, and early complex human behavior and culture. This lost *palaeoscape*, what we have called the Palaeo-Agulhas Plain (Marean et al., 2014), is now hidden but, because sea levels were predominantly lower through most of the Quaternary, it would have been an important, and we argue pivotal, now extinct ecosystem.

Recently, Carr et al. (2016) opined that "the nature of the vegetation on the continental shelf remains a critical unresolved element for interpretations of both the human and faunal records in this region …" partially due to "the poorly defined nature and distribution of continental shelf substrates" (page 38). In prior papers, we outlined a research agenda and methodology for tackling these palaeoecological puzzles (Franklin et al., 2015; Marean et al., 2015) and offered some preliminary hypotheses of the PAP character (Marean et al., 2014). With those hypotheses, we sketched a biophysical environment that set it apart from the other well-known CFR physiographies, and, therefore, we gave it a formal name – the Palaeo-Agulhas Plain (PAP). We then built a research team that, in this special issue, provides much of the information Carr et al. (2016) lament the lack of, and use it to build a model of that 'unresolved vegetation'.

In 1979, the seminal *Serengeti: Dynamics of an Ecosystem* (Sinclair and Norton-Griffiths, 1979) was published, and this groundbreaking synthesis of a migration ecosystem created a science model for future generations aspiring to fathom the complexities of abiotic and biotic interactions on a regional scale. The CFR was subject to similar treatment in 1992 with *The Ecology of Fynbos: Nutrients, Fire, and Diversity* (Cowling, 1992). Important updates have followed (Allsopp et al., 2014) and now we have deep and sophisticated understandings of these ecosystems. As palaeoscientists, we must aspire to reach such complex understandings of palaeoscapes as our fellow scientists have assembled for their modern ecosystems. Overall, we think the PAP resembled its far northern kin, the Serengeti, more than its neighbor next door, the contemporary CFR.

While we see the interdisciplinary study and understanding of these modern ecosystems as aspirational goals for the palaeosciences, we think we have brought to the table something that perhaps even these modern studies have yet to attain – a nearly fully coupled abiotic-biotic-human behavior computer model of the PAP. Marean et al. (2015) described a research agenda where palaeoscientists would develop linked computer simulation models, constantly under improvement, that would begin with models of land, sea, geology, soil, and climate. The majority of the abiotic characteristics would come from field and laboratory study, while climate would be projected using climate modeling validated using palaeo-archives. We would then employ vegetation modeling (Franklin et al., 2015) to project the flora across this modeled palaeoscape, and again validate those projections with palaeo-archive data. Since our study had a strong paleoanthropological objective, we proposed reconstructing a *resourcescape* for humans – a resourcescape is a formal model, built on the vegetation model, of the spatial distribution of resources sought by humans (food, water, wood, etc.). Finally, we would employ agent based modeling guided by the principles of behavioral ecology to model the behavior of ancient people in this ecosystem. We would then test the behaviors predicted by the model with the archaeological record. This volume and the papers in it provide some of our first research results from this approach applied to the PAP.

In this paper, we present a model of the PAP's abiotic and biotic characteristics and changing palaeoecology from marine isotope stage (MIS) 6 through 1 (around 195ka to the present). In so doing, we address the following research questions: 1) What was the ecology of this now extinct coastal ecosystem, and how did it compare to the contemporary coastal forelands of the CFR? 2) How did it vary through time and space? 3) What is its significance for understanding modern plant and animal biogeography? 4) What resources did it provide the early modern humans who exploited it, and how does this help us understand the human origins record? We set the stage for this model with a review of our growing knowledge of the PAP.

2. Background

As part of a national effort to assemble knowledge of its geological resources and map its offshore topography, South Africa and the University of Cape Town initiated the SANCOR Marine Geology Programme in the mid-1960s. From that work, R.V. Dingle, J. Rogers and others began publishing a series of descriptions and interpretations of the "triangular-shaped continental margin" called the Agulhas Bank. This resulted in a preliminary geological and topographic map of the Agulhas Bank and a reconstruction of the sedimentary history (Dingle, 1970a, b; Dingle and Rogers, 1972; Leyden et al., 1971; Rogers, 1971a, Rogers, 1971b; Slater, 1970). Dingle and Rogers (1972: 155) clearly recognized the broad significance of this underwater feature when they presented a "palaeogeographical background against which other scientific disciplines, for example, archaeology, botany, meteorology and zoology, etc., can view Pleistocene phenomena at the southern tip of Africa". At that time, a growing understanding of sea level heights was emerging, and while Dingle and Rogers recognized that there were multiple Pleistocene regressions, they opted for a general glacial palaeogeography, and they outlined a basic model of a variable plain exposed during three low sea levels: −140 m, −100 m, and −50 m.

Their palaeogeography is illuminating. They reconstructed the Breede, Gourits, Keurbooms, and Gamtoos rivers flowing across the PAP as broad alluvial flood plains of a type unknown in the CFR. They recognized a basic distinction between the western (west of Cape Agulhas) and central PAP, with the west largely a low-nutrient landscape, being underlain by ancient (Table Mountain Group), hard rocks and in some areas having substantial relief. The central landward area was described as having a wide strip of Mesozoic rocks producing relatively fertile, clayey soils that would have supported a more productive vegetation and a more diverse and dense fauna of herbivorous mammals than the west. They envisaged the southern margin as a level plain of calcareous rocks comprising a less productive landscape than the northern sector.

Shortly after this original SANCOR work became available, the first important publications appeared on the fauna from radiocarbon-dated excavations of caves and rockshelters along the coast. The research at Nelson Bay Cave (Fig. 1) was seminal because the site preserved an outstanding sequence across the Pleistocene and Holocene boundary, where the effects of the submergence of the PAP were readily apparent in the faunal assemblages. The analysis and publication of the large mammal fauna from Nelson Bay Cave (Klein, 1972b) was a Quaternary science landmark for its novel faunal analysis methods, and the recognition of a major faunal change at the Pleistocene-Holocene boundary. That same year a report (Klein, 1972a) was published on the excavations at Nelson Bay Cave that reproduced a map of the offshore topography (Slater, 1970), with Klein noting that the lack of shellfish in the Pleistocene sediments was likely due to the far distance to the coast. This was followed by publication of the large mammal fauna from Klasies River (Klein, 1976), and with these two sites, Klein was able to assemble a composite sequence of faunal change on the Cape south coast spanning ~110 ka through the Holocene (Klein, 1972a, Klein, 1972b, 1974, 1983). Klein (1983) points out that the faunal change at the Pleistocene-Holocene boundary exceeded faunal turnovers elsewhere in Africa. Janette Deacon (1978), having studied the stone tools from Nelson Bay Cave, assembled a composite figure (Deacon, 1978 Figure 12: page 105) of changing stone tool, bone tool, and large mammal (importantly terrestrial and marine) frequencies. It became a classic in African Stone Age studies, showing the Pleistocene with a bladelet-dominated stone tool industry (Robberg), large-bodied extinct and extant grazing fauna, and low frequencies of bone tools. This was replaced at the Holocene boundary by a flake-dominated stone tool industry (Albany), replacement of grazing species by a shrubland, mainly browser fauna, with the eventual addition of marine mammals, and an increase in bone tools. Deacon related this faunal turnover and shift in human adaptation to changes in sea level and distance to the coast. Deacon also was the first to cite R.V. Dingle and J. Rogers (1972), which had hitherto been ignored in the archaeological literature.

The 1980s saw B.W. Flemming and A.K. Martin (Flemming, 1983; Flemming et al., 1983; Martin and Flemming, 1986, 1987) publish on geological features such as the complexity of the offshore dune systems and the Holocene sediment wedge. A transformative paper (Van Andel, 1989) published a detailed topographic map of the Agulhas Bank which allowed estimates of the distance to the coast from anywhere along the Holocene coastline under several important sea level low-stands. Van Andel made the key observation that there were three basic states of the plain driven by sea level rise and fall: 1) when the plain was very wide and the coast far from the Holocene coastline, 2) when the plain was rather narrow but still present, and the coast was several kilometers away from the Holocene coastline, and 3) when the plain was totally submerged and the coast was where it is today or even higher (Van Andel, 1989: 140).

Following largely on the observations of Van Andel, our research group based at Pinnacle Point began a concerted effort to build a better understanding of the PAP. Erich Fisher led an effort to build a GIS computer model of the PAP landscape that joined topography and the sea level curve. The results of that effort were first used to test optically stimulated luminescence (OSL) age estimates of coastal resource use during MIS 6, which the model validated (Marean et al., 2007). The full model and its implications were published in 2010 (Fisher et al., 2010) and validated with dated strontium isotope measurements on speleothems. That model allows an estimate at any site along the Cape south coast of the distance to the coast across the PAP at 1500 yr time steps from ~420 ka to the present.

That same year we published a speleothem isotopic study from Pinnacle Point that spanned MIS5-3 (Bar-Matthews et al., 2010). Our goal was to begin to assemble long, continuous high resolution and tightly dated records of climate and environmental change, and specifically to track changes in C_3 versus C_4 grasses and winter versus summer rain. Speleothems are excellent for doing this (McDermott, 2004). In the CFR, grasses using the C_3 photosynthetic pathway associate with winter rain in the west and grasses with the C_4 photosynthetic pathway with summer and bimodal rainfall to the east (Cowling, 1983; Vogel et al., 1978). The speleothem results suggested that during MIS 4–3, summer rain and C_4 grasses expanded onto the exposed Agulhas bank and adjoining part of the contemporary coastal lowlands (CCL). Using some basic relationships between Cape vegetation, geology, altitude, annual rainfall, and season of rainfall, Bar-Matthews et al. hypothesized that during MIS4-3, a grassy vegetation type with more C_4 grass types than common in the region today may have existed on the adjacent exposed Agulhas bank. Such C_4 grasslands form a nutritious grazing resource (Pratt and Gwynne, 1977; Tainton, 1999) and thus could help account for the abundance of large-bodied grazing taxa. An isotopic analysis of three grazer specimens from Last Glacial Maximum (LGM) deposits at Nelson Bay Cave displayed values indicating “significant C_4 grass component” (Sealy, 1996). For the first time, there was concordant evidence that C_4 – dominated grassland would have been present on the bank during colder phases.

Based largely on these emerging results, combined with basic grassland ecosystem ecology, Marean (2010) proposed that the exposed Agulhas bank, sitting at the footsteps of the major modern human origins sites along the coast, would have been highly significant to the hunter-gatherer foraging system. Marean proposed that the large grazing ungulates so prevalent in the Pleistocene faunal assemblages were largely restricted to the exposed Agulhas bank. Assuming summer rains to the east and winter rains to the west, an ungulate migration ecosystem was hypothesized, with grazers moving east in the summer and west in the winter, chasing nutritious green grass and leaving behind the dry grass in the dry season. People living in the archaeological sites of the Cape south coast were well positioned to intercept these migrating herds twice a year as they passed by. Combined with access to the coastal resources and a diverse and productive flora of the CFR with underground storage organs (USOs), south coast hunter-gatherers would have had a trio of rich foraging resources that would have had many downstream implications. Scientists sometimes assume that glacial phases provide “harsh” environments for hunter-gatherers. Marean, however, argued that the productivity of both the coastal resource base and the diverse and abundant geophyte flora was either resilient to, or even increased, during colder climates. As sea levels retreated during these glacial phases, humans added large grazing ungulates to the resource base, making this region a potential refugium during glacials (Marean, 2010, 2011, 2016).

Compton (2011) drew on the earlier geological mapping of Dingle and Rogers (1972) to propose a basic vegetation model of the PAP under maximum glacial conditions. He argued that Pleistocene hominins on the PAP would have been isolated during glacial phases and thus subject to allopatric evolution, and then subjected to intense pressure during periods of rising sea level. During these phases, according to Compton, natural selection would have been intense and when combined with the effects of genetic drift caused by isolation, these groups would have diverged from more inland groups. When reconnected with the inland groups, positive adaptive traits would have spread. More generally, Compton pointed to now submerged landscapes as being significant to human evolution.

Recognizing the critical need for more and detailed information on the PAP, Hayley Cawthra commenced a PhD program on the geophysics of the PAP immediately adjacent to Pinnacle Point at Mossel Bay. She used the best available offshore geophysical methods combined with samples attained through diving, and petrographic characterization and OSL dating of the samples, to significantly improve our understanding of the PAP (e.g., Cawthra et al., 2018, 2020a [this issue], 2020b [this issue], 2020c [this issue]) Importantly, that study was part of a large organized transdisciplinary study of the PAP by the research group represented in this special issue. The germination for that effort occurred at the Fynbos Biome Workshop in 2012 that later resulted in the edited volume *Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region* (Allsopp et al., 2014). Palaeo-scientists and evolutionary biologists attending that workshop recognized the concept and significance of the PAP. A research strategy for investigating and reconstructing its nature was developed. Two years later that group identified the PAP as a new ecosystem and one that added an entirely new dimension to the CFR, and they outlined a qualitative model of its characteristics, and integrated it into the narrative for South African archaeology (Marean et al., 2014). Tests of some of these ideas have appeared. An analysis of age at death of extinct blue antelope from a sample of sites along this migration route is consistent with migratory movement (Faith and Thompson, 2013). After building a strontium isoscape, it was found that all the grazing ungulate taxa in the Pleistocene Pinnacle Point record lived on the PAP, and did not move off the plain in any significant manner into the interior (Copeland et al., 2016).

3. Approach

Our approach to developing a palaeoecology of the PAP, and illustrated in this volume, follows the framework outlined in Franklin et al. (2015) and Marean et al. (2015). Our research plan had as a major part of its goal a better understanding of human adaptations in this region and, therefore, our palaeoecology targeted the development of a resourcescape for hunter-gatherers. That resourcescape would be the basis for a quantitative model for the modern environment of resource return rates across the landscape for resources such as plant foods, animal prey, and raw materials for stone tools, and heating and cooking. Next, we use that model as a basis for projecting resourcescape models under different climate conditions in the past. The goal was to predict how a human forager would use this environment under differing climate conditions of the Middle and Late Pleistocene.

Our framework (Fig. 2) had at its core two new approaches for understanding the past. First, we reversed the normal approach to reconstructing palaeoenvironments. This approach begins with a palaeoarchive, such as a speleothem, lake core or hyrax midden. These palaeoarchives are described and then the descriptions are generalized outward from that location as a regional palaeoenvironmental reconstruction. Additional paleoarchives are introduced and theories of environmental reconstruction are adjusted *ad hoc* to accommodate any contradictions, inductively. We argued for a reversal to this strategy that would harness newly available climate and environment modeling capabilities and would explicitly depend on a widely transdisciplinary approach. We proposed to use computer models to project landscape level maps of past climate and environment rather than extrapolating from point-based empirical studies of palaeoarchives. Since our target region has such a variable landscape and seascape due to the dynamic PAP, and the coastline seems so important to the human foragers, we conceptualize both together as a *palaeoscape*. Our proposed research strategy begins with a reconstruction of the abiotic characteristics of the target region through: 1) geological, geophysical, and GIS studies to create a rock and soil topographic base map (Cawthra et al., 2020a [this issue], 2020b [this issue], 2020c [this issue]); Fisher et al., 2010), and 2) using a regional

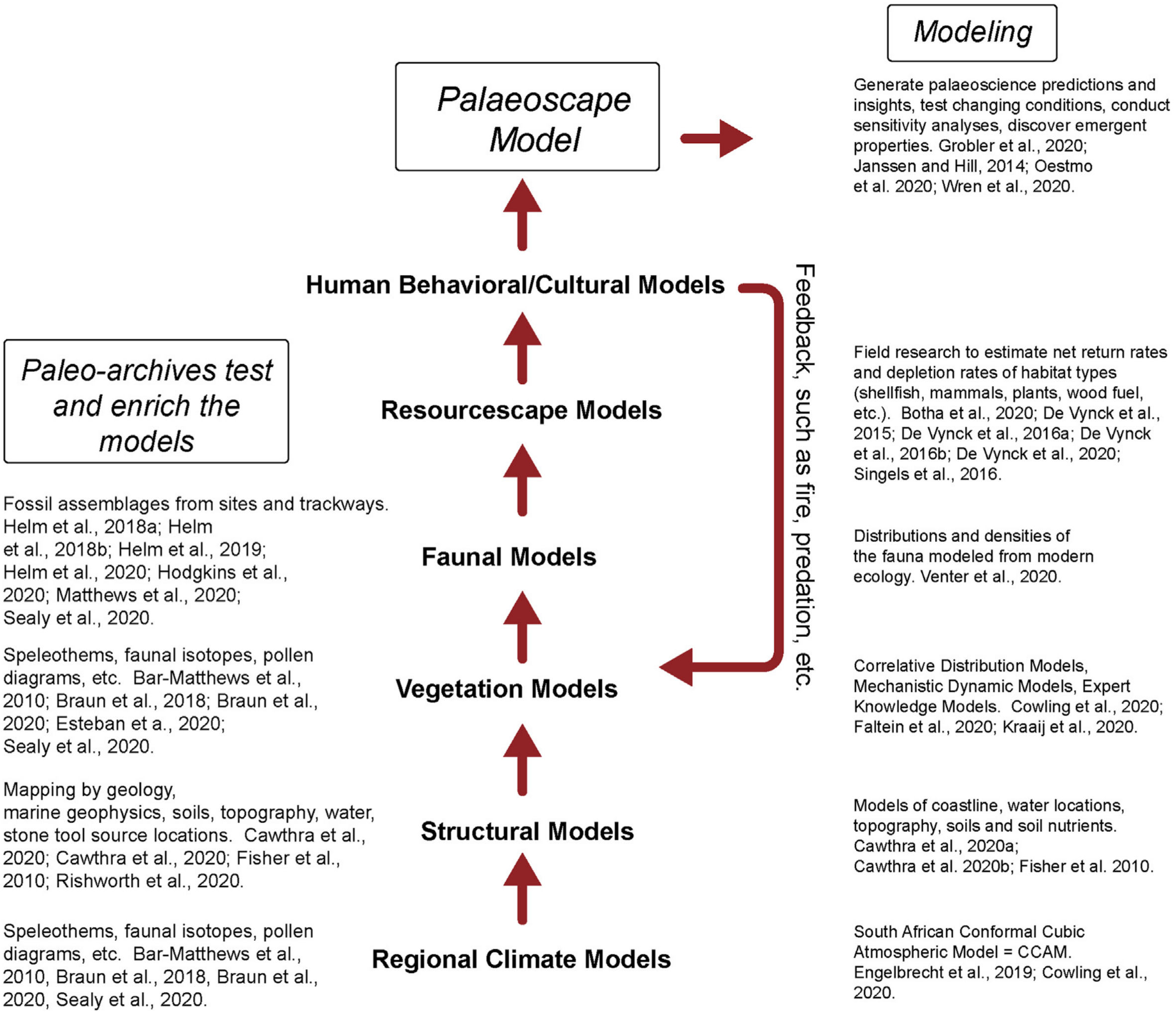

Fig. 2. This diagram shows the workflow of the Palaeoscape approach, and specifically the workflow applied to reconstructing the Palaeo-Agulhas Plain. On the right side are the descriptions and workflow of model creation. On the left side are studies from palaeo-archives used to test and enrich the output of the modeling. The citations only include those studies that were part of this project or in this special issue.

climate model to create predicted palaeoclimatic conditions (Engelbrecht et al., 2019). These data are then used with vegetation models to project a vegetation map of the various biomes and major vegetation types (Fynbos, Grassland, Renosterveld, etc.) across the palaeoscape (Cowling et al., 2020 [this issue]). This workflow creates our palaeoenvironmental model, and we then deduce predictions from that model to test and enrich with palaeoarchives. An obvious advantage of this deductive approach is that there are formal principles employed to extrapolate the spatial extent of vegetation and habitat types.

Secondly, we proposed to make predictions of past human behavior from formal principles and methods. Archaeologists regularly make predictions about how humans behaved in the past. Normally they are derived from a combination of qualitative characteristics of the environment, ethnographic observations of people living in the same or similar environments, tied together with common sense. The classic regional example of this is J. Parkington's seasonal mobility model (Parkington, 1980, 1981, 1984). In the last 20 years, there has been a revolution in computer modeling of human behavior, largely due to widely available increases in computational power and modeling tools such as Agent Based Modeling (ABM). We proposed to use formal economic principles as manifested in behavioral ecological theory (Stephens and Krebs, 1986) and operationalized with ABM (Janssen and Hill, 2014). We defined the returns of foraging in a particular habitat type as equal to the return rates that come from ethnographic and experimental studies of foraging (Botha et al., 2020 [this issue]; De Vynck et al., 2015, 2016a, 2016b, 2020 [this issue]; Singels et al., 2016). In this volume, we illustrate the utility of this approach at two scales. Oestmo et al. (2020 [this issue]) show how this approach can be used to address a very specific question – how do we predict what stone tool raw materials a forager should choose to use? A major utility of the ABM approach is that we can ultimately take very specific models that address issues like raw material choice for stone tools and ochre, and large mammal hunting, and build them into a fully integrated ABM model that simulates overall adaptation. Wren et al. (2020 [this issue]) provide an example of our first generation model of the Holocene landscape with the PAP removed. In the future, as the PAP resourcescape is assembled, we will move to simulations that encompass glacial climates.

In the following section, we employ this approach by synthesizing the many contributions in this volume into a general conceptual model of the PAP. We tap synergies between these studies that allow us to build a reasonably confident palaeoecological model of the PAP. Where possible, we use archival records to enrich the projections. We also make some suggestions as to what the character was of other glacial states of interest to our broader goals, namely MIS 6 and MIS 4. As illustrated by Wren et al. (2020 [this issue]), we are well advanced in developing a formal palaeoscape model for the Holocene, but we still need more details before we can advance the glacial state model from the informal state to the formal. That will come in the near future. That being said, all models begin in the informal state, sometimes as sketches or drawings, other times as narratives, or both.

4. A general model of the PAP during the Last Glacial Maximum

Topographically and edaphically, the PAP comprised a landscape without analogue in the extant CFR. Fig. 3 shows a reconstruction of this palaeoscape. The relief was subdued and the region dominated by deep and relatively fertile soils compared to the CFR. Wide (up to

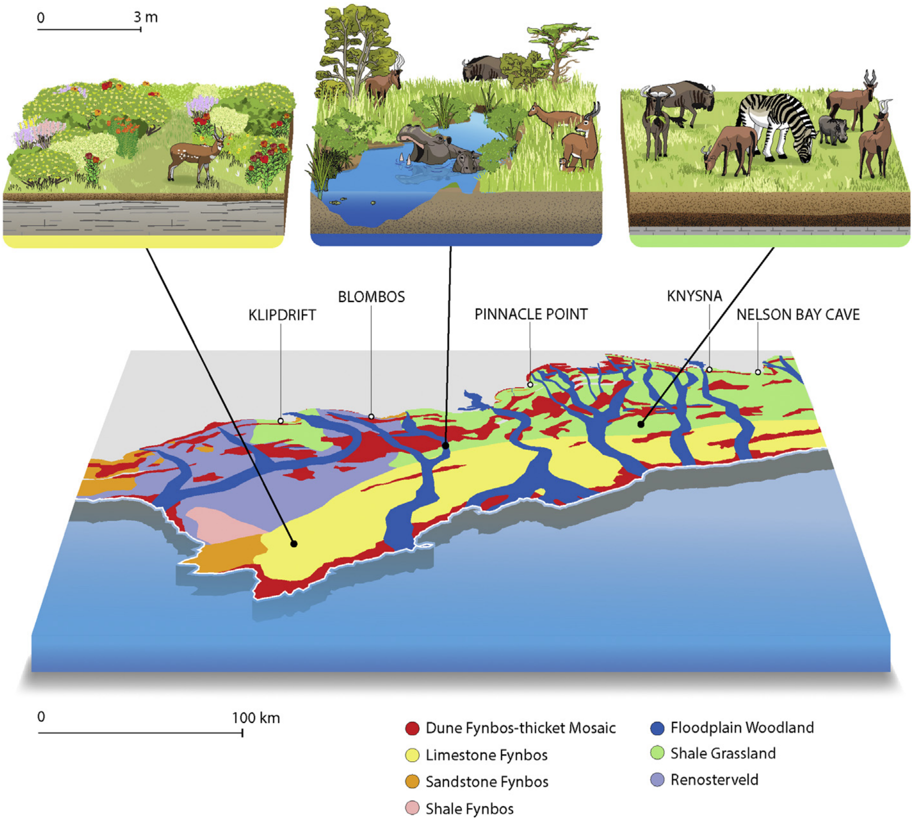

Fig. 3. The major environments of the Palaeo-Agulhas Plain relative to some of the significant human and palaeo-archive sites. The panel below shows a redrawn version of the Last Glacial Maximum vegetation model as produced by Cowling et al. (2020 [this issue]). The panel above shows schematics of the flora. and fauna. Figure by Patrick Fahey.

30 km) and shallow river valleys traversed the entire plain and these broadened as they went seaward. Alluvium that yielded deep and fertile soils filled these valleys. These covered 15 000 km^2, an eight-fold increase from today's CCL. Unlike the current CFR, wetlands were widespread in the flood plains and along the coast. Our research has demonstrated significant physiographic variation across the PAP and, therefore, we have identified several zones that were relatively homogeneous ecologically (Fig. 1). Our primary focus is the central plains where we have concentrated much of our research in and about the Mossel Bay environs, and more recently near Knysna.

4.1. Abiotic characteristics

The PAP, when fully exposed as it was during the lowest sea level heights of the LGM, was extensive, and roughly doubled the size of the current CFR (Fisher et al., 2010; Van Andel, 1989). The western and central plains were regularly 90 km or more from the coastline, while moving onto the far eastern plains near Port Elizabeth it eventually pinched down to 10 km or less. During periods when the PAP was extensive, fog and other forms of coastal-sourced moisture were significantly less on and about the caves and rockshelters. This was detected in strontium isotope analysis of dated speleothems from Pinnacle Point, showing lower influence of sea-sourced strontium during times when the coast was further away (Fisher et al., 2010). Karkanas et al. (2015) documented the impact of this changing sea-sourced moisture, showing that during times of heightened sea level and sea-sourced moisture, there was rapid exfoliation and deposition of the cave and rockshelter roof spall, while during sea retreats this spalling slowed appreciably and aeolian deposition became the primary source of sediment. The lowered water table made the caves and rockshelters significantly drier, improving the preservation of organics in the archaeological sites, and the seeps of fresh ground water that are typical of the current coast would no longer be close to the caves and rockshelters. Since the mean daily foraging radius of hunter-gatherers is around 10 km (Marlowe, 2005), coastal resources would be outside the range of people inhabiting the current *neo*-coastal caves and rockshelters during these strong regressions in areas where the plain is wide.

The topography was predominantly flat to gently rolling, depending on the form of dunes that would have been fixed by vegetation, particularly in the eastern and central plains (Cawthra et al., 2020b [this issue]). The western plains had somewhat more topographic relief. The lack of significant topography lessened the impact of aspect-related energy regime on vegetation. This broad flat plain provided few obstacles to weather systems or wind. People could see prey or enemies across long distances. There were few exposed rocky hills, cliffs or inselbergs, so there was little fixed shelter like caves or rockshelters for humans to exploit. This relatively flat terrain was gently dissected by meandering, sometimes broad and braided, streams and rivers trending predominantly north-south. On the western plains, the Breede River turns abruptly west where the Sout and Heuningnes Rivers join it, which must have made this a powerful downriver drainage during the wet season. These streams and rivers were more structurally controlled near the *neo*-coastline, where they were narrower, but then as they drained outward onto the plain they broadened significantly. Draining the interior, they would have risen and sometimes flooded during the rainy season. To the west, these would have risen strictly during the winter since the interior was largely winter rainfall, but to the east, the rising waters would have been increasingly bimodal, resulting in potentially longer periods of wet and waterlogged landscapes.

While most plains environments are relatively easy to traverse, the abundance of north-south drainages may have made east-west movement more challenging on the PAP. The regular flooding would have consistently replenished the soil and produced a landscape rich with alluvium (Cowling et al., 2020b [this issue]). Since the channels were typically 20–40 km distant from each other, they were a relatively short walk for people and animals on much of the landscape. Combined with the presence of fresh-water seeps (Rishworth et al., 2020 [this issue]), fresh water was regularly available on the plains to people and animals. Nearer to the coast in the southern plains, these would have been broad and soft sandy estuaries and vast wetlands with huge potential for migratory birds and estuarine fish. Long dissipative beaches would have dominated the coastline, providing rich sources of sand mussel (*Donax serra)* in the sands, and in some areas, beachrock, and aeolianite reefs for mussels, limpets, and alikreukel or giant turban (*Turbo sarmaticus)* (Cawthra et al., 2020a [this issue]) Sufficiently far upstream, where the water was fresh, there would have been rich habitat for crocodiles and hippos (Helm et al., 2020 [this issue]). These regular sources of water would have made outstanding ambush hunting opportunities for predators of all types.

The PAP's geology and soils differed dramatically from that found in the modern CFR landscapes (Cawthra et al., 2020b [this issue]), and the northern and southern plains differed from each other. The southern plains, comprising an area of 22 000 km^2, was geologically monotonous, dominated by Neogene limestone and calcareous dune sands at the coast. Devonian shales and Cretaceous mudstones dominated the 14 000 km^2 northern plains, with capping of calcareous aeolianites stranded by changing sea levels. Broad, alluvial valleys traversed both of these sectors as described above. The quarzitic sandstones that dominate the Cape Fold Belt of the onshore CFR were restricted to the extreme west, as was an exposure of volcanic rocks produced in response to the rifting of the Falkland and African plates in the Mesozoic. Clay and loam soils dominated the northern plains with clays more abundant to the west. Overall, soils on the northern plains were deep, tending to be neutral in pH, with moderate to high fertility. On the southern plains, soils were shallower, tending toward alkaline, and moderate to low in fertility. The alluvial soils of the river valleys were likely deep and highly fertile loams.

To model LGM climate over the PAP, eight coupled global climate model projections of LGM climate were downscaled to 8 km resolution using the regional conformal-cubic atmospheric model (CCAM) (Engelbrecht et al., 2019). The LGM climate of the PAP was colder than today but not markedly so, with temperatures on the plains ranging 2–4 °C cooler for both the western and central plains (Engelbrecht et al., 2019). The seasonal cycles differed somewhat from today on the CCL, with winters in the central plains being colder than today and summers more similar in temperature to today. The simulations suggest, like today on the CCL, there was a very low probability of frost. The western plains were significantly wetter than today on the CCL, while the central and eastern plains were slightly drier. In the west, much of this rainfall increase is attributable to stronger winter rains, and the drier climates of the central plains are largely a function of reduced winter rain; however, central and eastern plains received more warm-season rain than today, concentrated mainly in the warmer spring and autumn months. Overall, the majority of the PAP was drier, less windy, received less winter rain and warm season (spring to autumn) rain. We discuss the impacts of these abiotic features on the biotic character of the ecosystem below.

4.2. Terrestrial habitat characteristics during glacial conditions

(Cowling et al., 2020 [this issue]) developed a rule-based vegetation model for the Cape south coast and validated the model with comparisons to modern vegetation. They then took the output of the downscaled regional climate model (Engelbrecht et al., 2019) and applied a bias correction. This bias-corrected climate output was combined with geological and soil characteristics of the region during low sea level (Cawthra et al., 2020b [this issue]), and corrections for the likely effects of low atmospheric CO_2 and lower temperature, characteristic of the LGM, on plant water use efficiency. These data drove the rule-based model to generate a vegetation model of glacial conditions of the LGM.

The overall character of the PAP differed from the current CCL. The repetitive transgressions and regressions through the Pleistocene (Fisher et al., 2010; Van Andel, 1989) left a legacy of marine sediments on the plains. Limestone fynbos and dune fynbos-thicket mosaic, both associated with marine sediments, thus were dominant vegetation types on the modeled PAP landscape. These sediments and vegetation types are rarer on the CCL, and therefore the high diversity of plants, especially edaphic endemics, in these vegetation types (Cowling, 1983; Willis et al., 1996) may be a legacy of their once larger extent on the PAP (Grobler et al., 2020 [this issue]; Marean et al., 2014). Overall, the PAP differed from the CCL in having expansive areas with fertile to moderately fertile soils that supported floodplain woodland and shale grassland. “Sweet” (nutritious when dormant) grass species would have dominated these areas. Woodlands surrounded floodplains, while grasses and sedges would have dominated the seasonally flooded areas. The perched hardpans and calcretes would also have had grass and sedge vegetation.

Using LGM climate parameters, (Kraaij et al., 2020 [this issue]) predict that the region would have experienced conditions suitable for the spread of wildfires more frequently than under contemporary conditions. For example, at Cape Agulhas the number of days having a high McArthur Fire Danger Index was predicted to be 5–10 times greater (up to 105 days per annum) during the LGM than at contemporary times. The center of the PAP was predicted to have between 89 and 106 high-danger days at the LGM; values decreased eastwards but were still higher than at present (Kraaij et al., 2020 [this issue]). We can expect that fire was an important ecological factor during the LGM that likely helped maintain the grasslands, because the study area was occupied by humans who likely used fire to increase plant foraging returns (Botha et al., 2020 [this issue]; Deacon and Deacon, 1999), to enhance plant palatability for attracting game (Marean et al., 2014), and the PAP largely lacked topographic barriers to the spread of fire. Future simulations will explore this topic further.

In the remainder of this section, we describe the regional variation of the PAP while integrating the predictions of the vegetation model with the vertebrate fauna of the PAP, for which there is good fossil evidence to reconstruct community structure of mammalian herbivores. Our characterizations of the behaviors and habitat types of the extant herbivores rest largely on Estes (1991) and Kingdon (2015), except where we note specific details not found in those references and cite other papers. We rely on Skead, 2011 for information on historical distributions of the mammals. In our summaries of the fossil occurrences of the large mammals from the Cape south coast, we rely on (Klein, 1972b, 1976, 1980, 1983, 1984) for Klasies River and Nelson Bay Cave, Rector and Reed (2010) for Pinnacle Point, summaries given in Marean et al. (2014), and (Badenhorst et al., 2016; Henshilwood et al., 2001) for Blombos. Our summaries of the trackway evidence relies on recent research led by Helm (Helm et al., 2018a, Helm et al., 2018b, 2019, 2020 [this issue]). Note that only Nelson Bay Cave currently provides a sample of LGM fauna.

The cave and rockshelter paleoarchives (Klasies River, Nelson Bay Cave, Pinnacle Point, Blombos, and Klipdrift) that sample the PAP sit at the boundary of the CCL and the PAP. The vegetation model suggests this would have been an ecotone where vegetation would have transitioned due to edaphic changes, but rainfall would not. The primary archives from those sites include the following. Cave speleothems sampled the rainfall and vegetation at this ecotone (Bar-Matthews et al., 2010; Braun et al., 2018, 2020 [this issue]). Fossil trackways are almost all in coastal aeolianites (dunes) exposed near shore and thus sampled the movement of animals near the juncture of the CCL and PAP (Helm et al., 2018a, Helm et al., 2018b, 2019, 2020 [this issue]). Ancient phytoliths from the paleoarchives reflect plants brought in by occupants of the sites and some natural windblown input (Albert and Marean, 2012; Esteban et al., 2017, 2020 [this issue]). The micromammals in the paleoarchives were accumulated by owls and small carnivores, and represent a local sample of a community no larger than a ~2 km radius (Avery, 1982, 1986; Faith et al., 2018; Matthews et al., 2009, 2011, 2020 [this issue]; Williams et al., 2020 [this issue]). Hyenas and humans accumulated large mammals that reflect a much broader sampling radius that could be as large as ~20 km (Klein, 1972b, 1976; 1983; Rector and Reed, 2010). The bulk isotopes from those large mammals reflect a mean across the formation time of the sampled tooth (Sealy et al., 2020 [this issue]; Williams et al., 2020 [this issue]), while the serial isotopes provide a reflection of seasonal changes in diet due to local seasonal shifts in vegetation and animal movement (Hodgkins et al., 2020 [this issue]). Research on ancient paleosol systems preserved as remnants of the far northern extent of the PAP at Vleesbaai (Oestmo et al., 2014; Smith et al., 2018) and Blombos (Jacobs et al., 2020 [this issue]) will eventually provide further evidence on the PAP.

The vegetation model predicts that during glacial periods much of the Holocene coastline was an ecotone between various forms of fynbos and forest on the CCL and grassland and renosterveld on the PAP. A significant exception to this is the region between the Great Brak River and the Mossel Bay Point, where the grasslands extended inland (Fig. 3). This ecotonal character of the caves and rockshelters is displayed in the micromammal assemblages from these sites (Avery, 1982, 1983; 1986, 1987; 1999; Faith et al., 2018; Matthews et al., 2009, 2011, 2020 [this issue]; Williams et al., 2020 [this issue]) and their isotopes (Williams, 2015; Williams et al., 2020 [this issue]) throughout the Pleistocene. All show a stable pattern signaling vegetation typical of the modern Cape, plus evidence for grasslands. Matthews et al. (2020 [this issue]) attribute this stability and resilience of the micromammal assemblages to the wide tolerance most of these animals display, and the fact that the local vegetation is driven strongly by geology and topography, which has not changed significantly.

A dominating feature of the PAP was the presence of broad meandering streams and rivers fed by upriver rainfall and the sediments they incised, regularly depositing alluvial sediments onto the plains (Cawthra et al., 2020b [this issue]). These cut through the northern and southern plains and were present the entire west to east extent. This created long and broad zones of floodplain woodlands which likely included numerous wetlands that supported herbaceous (mainly grasses and sedges) vegetation (Cowling et al., 2020 [this issue]). These valleys would have likely comprised a mosaic of grassland and a grassy woodland dominated by *Vachellia karroo*, a high quality fire-wood (Van Wyk and Van Wyk, 1997; Van Wyk et al., 2000), the latter showing strong similarity to subtropical savanna. This habitat, probably the most productive for larger mammals on the PAP, would have been home to browsers such as *Tragelaphus scriptus* (bushbuck) and *T. strepsiceros* (greater kudu), *Giraffa camelopardalis* (giraffe), *Diceros bicornis* (black rhino), a diversity of grazers using the grassy under-story, as well as mixed feeders such as the springbok species (*Antidorcas marsupialis* and *australis*), and *Taurotragus oryx* (eland). The Pleistocene fossil assemblages and trackways document the presence of most of these.

Redunca arundinum, the southern reedbuck, are common in the Pleistocene faunal assemblages. This species is presently associated with flooded grassland and wetlands of tropical south and central Africa, reaching Kwa Zulu-Natal in the southeast. It likely thrived on the floodplain grasslands, moving off to surrounding grassy areas during the floods, and back when the water receded. *Hippopotamus amphibious*, the common hippo, and *Crocodylus niloticus*, the Nile crocodile, would have been plentiful, and their trackways have been identified in the Pleistocene sediments while their remains are largely absent in the fossil assemblages. *Loxodonta africana* (elephant), well represented in the Pleistocene trackways but not the fossil assemblages, would have been a common visitor to these wetlands. Its abundance in the trackways suggests that it may have regularly moved between the PAP and CCL.

These floodplain grasslands would have been frequented by other grazing species such as *Alcelaphus buselaphus* (hartebeest), *Connnachaetes gnou* (black wildebeest), *Damaliscus pygargus* (bontebok), *Hippotragus equinus* (roan) and *H. leucophaeus* (blue antelope), *Equus quagga* (quagga) and *E. capensis* (giant extinct zebra). All are present in the Pleistocene fossil assemblages and some in the trackways. The hartebeest is a grazing generalist, foraging on short to tall grass, and it sometimes moves up and down riparian zones following its preferred forage. It is likely that the grasslands of the floodplain were tall and tussocky, thus providing southern reedbuck with one of its preferred habitats, whereas those of the shale- and mudstone-dominated interfluves were short, providing black wildebeest with its preferred forage. The Pleistocene fossil assemblages preserve the giant extinct buffalo *Syncerus antiquus* and its smaller extant cousin *S. caffer* (the Cape buffalo). The giant buffalo is a hyper-hypsodont species that had broad horns that stretched at least a meter perpendicular to its body, and the trackways show a foot consistent with this. This animal required treeless, grassy plains, otherwise it would have been immobile, so we expect it frequented the open flooded grasslands and shale grasslands. The Cape buffalo is more generalized in its feeding behaviors and would have thrived in all the grassy areas of the PAP, and this is reflected in its relative abundance in the fossil assemblages. The extinct giant alcelaphine, *Megalatragus priscus,* is present but rare in PAP Pleistocene assemblages. It is reconstructed as a specialized roughage grazer that was probably gregarious (Brink et al., 1995, 2015).

The extensive shale grasslands of the central and eastern sectors of the northern PAP would have fronted at times during the Pleistocene the sites of Klasies River, Nelson Bay Cave, and Pinnacle Point. Hartebeest, black wildebeest, bontebok, Cape buffalo, giant buffalo, springbok, roan, blue antelope, eland, quagga, and extinct giant zebra would have populated these grasslands. All but extinct giant zebra are present in the LGM assemblage at Nelson Bay Cave. The extinct giant buffalo is present in LGM assemblages, a testament to the presence of treeless grasslands in this vegetation. Roan also prefer treeless, short-grass plains, and their abundance in the LGM assemblages is consistent with an open short grassland. Increased summer rain would have increased the C_4 component of the grasslands, especially to the east, and the C_3 component would have increased to the west (Cowling et al., (2020 [this issue])). At Nelson Bay Cave in the Eastern Zone, the bulk sampling isotopes from the ungulates are interpreted to reflect an LGM grassland that is more C_3 relative to the Holocene (Sealy, 1996; Kraaij et al., 2020 [this issue]). At PP30, where both serial and bulk isotope sampling was conducted (Hodgkins et al., 2020 [this issue]; Williams et al., 2020 [this issue]), our results show that the bulk sampling procedure may not capture the full range of seasonal shifts between C_3 and C_4 grasses, and we expect that the extensive floodplain grasslands on the LGM PAP could also have substantial amounts of C_3 sedges.

Venter et al. (2020 [this issue]) used knowledge of modern ecosystems and ecosystem processes to build statistical predictions of the community ecology of the PAP. They found that the species representation from the fossil assemblages and trackways underestimates the expected species richness as modeled from modern ecosystems. Therefore, despite significant improvements in our samples we still need more field and laboratory research. Nonetheless, Venter et al. (2020 [this issue]) found similarities in species packing to the Serengeti, suggesting the PAP had a large mammal community reasonably typical of open, migratory, large herbivore ecosystems. It was hypothesized that these normally migratory animals may have migrated east and west following the seasonal march of rainfall (Marean, 2010). Hodgkins et al. (2020 [this issue]) conduct a test of the migration hypothesis using serial isotope sampling of ungulates from an MIS 6 age fossil community that dates to ~151 ka. Fig. 4 shows their data in a manner designed to illustrate the broad palaeoecology of the large ungulates. Southern reedbuck shows a pattern of $\delta^{13}C$ variation that is consistent with a lack of movement - and small annual variation – as expected of this non-migratory species. A second group of ungulates exceeds this range of variation and thus has a range of variation greater than the non-mobile southern reedbuck, and there is a smaller group that shows wide variation in diet that likely indicates significant movement. This suggests a mixed community of animals being sampled by the predator, in this case the scavenging brown hyena (*Parahyena brunnea*), where some ungulates are migratory, some move shorter distances, and others are resident populations of grazing species. These less mobile individuals likely used the local grasses in the woodlands and floodplains on a yearlong basis and this is why they dominate the assemblage while migrants are rare but present.

In the nearby Klein Karoo, separated from the PAP by the rugged Outeniqua Mountains, there was a Pleistocene grazing ungulate population contemporary to that on the PAP (Faith, 2013; Klein, 1978; Sealy et al., 2016). The strontium isotope analysis (Copeland et al., 2016) suggests that, at least around ~151 ka, the PAP ungulates did not move into the Klein Karoo. We think that the grazing ecosystems of these two areas were largely separate throughout the Pleistocene, and an east-west migratory movement of grazers in the Klein Karoo would be likely. Brink (Brink, 1992; Brink et al., 1995, 2015), who reconstructed the Middle and Late Pleistocene palaeoecology of the central interior of southern Africa as having a grazing succession, modeled his reconstruction on the well-known Serengeti ecosystem (Bell, 1969, 1971; McNaughton, 1985). In this hypothesized grazing succession, the first migrants graze down the tall grass, followed by the medium grass grazers, and then the short grass grazers. The range of anatomical morphotypes and body sizes that signals this type of facilitative niche separation identified by Brink in the central interior, and known to drive the East African systems, is well represented in the Pleistocene PAP. It thus seems likely that a grazing succession characterized a portion of the Pleistocene ungulate communities of the PAP. This abundance of large bodied grazers, combined with the regular presence of elephants (Helm et al., 2020 [this issue]), and fire (Kraaij et al., 2020 [this issue]), may have acted to maintain and spread grasslands on the PAP.

The western sector of the northern PAP, which was wetter than the east and enjoyed a strong winter-rainfall regime, supported shrubland vegetation more typical of the contemporary CFR. Shale fynbos and renosterveld prevailed, with patches of sandstone fynbos in the extreme west. The marine geology reveals a volcanic formation in a strongly winter rain area, and the vegetation model predicts shale fynbos for this area, with the potential for nutritious grass lawns. We stress that volcanic soils and winter rain is a rather

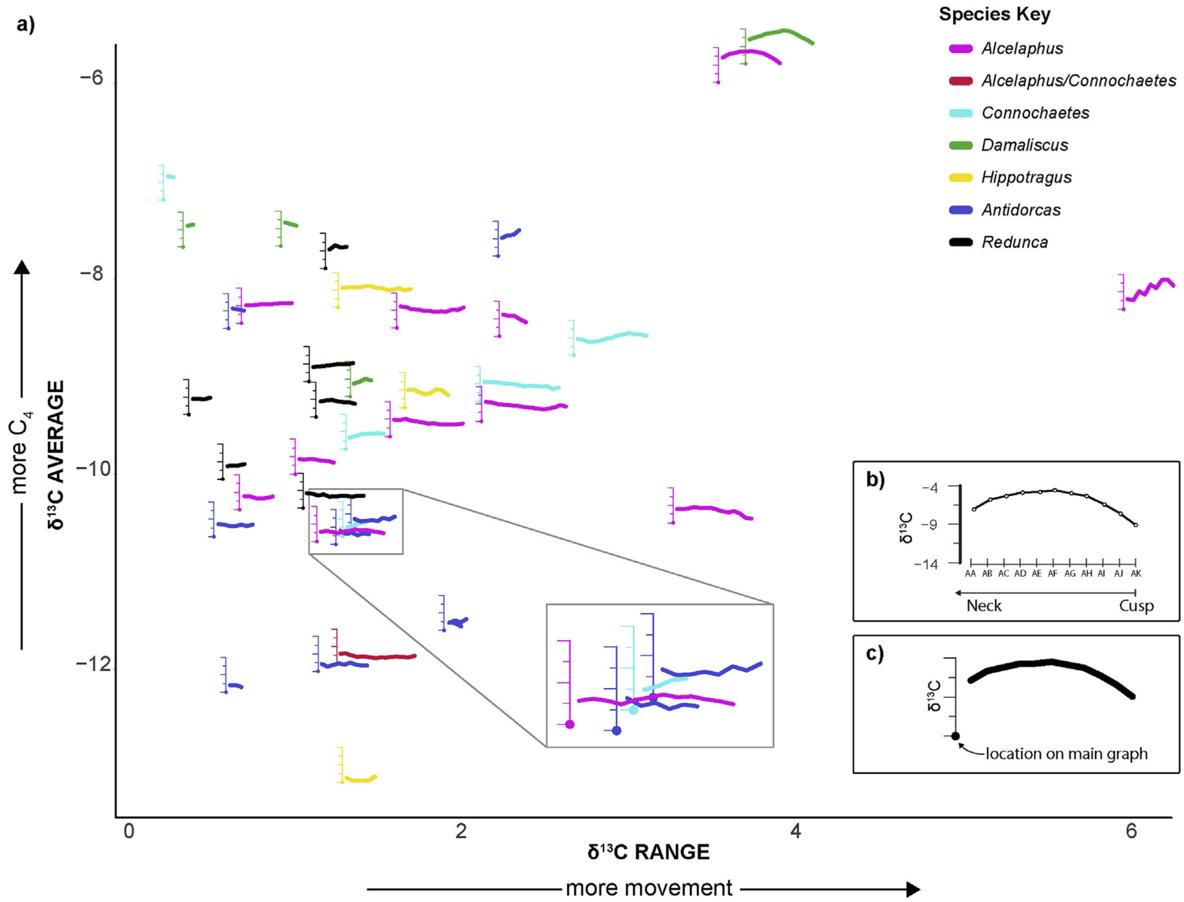

Fig. 4. The palaeoecology of the large ungulates of the Palaeo-Agulhas plain from serial drilling for isotopes a) The x-axis shows the range of drilled δ^{13}C measurements of an individual tooth, and the y-axis shows the average δ^{13}C of the tooth. Each small graph is a smoothed line across individual measurements from neck to cusp (as in b) and c), with b) showing a specimen with all the measurements and c) showing how it was smoothed. The individual small graphs are arranged along the x and y axes by the mean of their range and average δ^{13}C, respectively. The lines allow the reader to evaluate whether the changes in diet are temporally vectored or random. More dietary variation, and possibly movement, is to the right, while a greater component of C$_4$ grass is indicated to the top.

novel combination for this region so our vegetation model could underperform in that context. We lack an LGM faunal assemblage from this region to help project the faunal communities, but, along with the dune fynbos-thicket mosaic that was abundant throughout the northern PAP, it would likely have supported a mammal fauna typical of contemporary CFR shrublands, namely *Raphicerus melanotis* (grysbok), *Sylvicapria grimmia* (bush duiker), and bushbuck. The grassy component of renosterveld would have provided forage for black wildebeest, bontebok, Cape and extinct buffalo, roan, blue antelope, quagga and extinct giant zebra, and eland would likely have found the mixed habitat attractive.

The southern plains was a large homogenous region dominated by limestone fynbos intersected by extensive floodplain woodlands. This would have been a relatively unique combination for the CFR. This windswept shrubby environment is well outside the foraging radius of humans and animals living in the archaeological sites, and thus we do not have fossil assemblages that sample its character, and of course, no trackways. Upstream, our characterizations of the flooded woodlands and associated grasslands would apply here, but moving south the floodplains would become increasingly tidally influenced and brackish. This would be a constraint for large mammals, but would provide rich estuarine zones thick with birds and fish. Coastal dunes covered with dune fynbos-thicket mosaic would line these broad sandy beaches, and in all these areas grysbok, bush duiker, and bushbuck would be common.

4.3. The LGM compared to MIS 6 and 4

MIS 6 and 4 are glacial phases of intense paleoanthropological interest due to the likely origin of the modern human lineage in MIS 6, and the explosion of evidence for complex behaviors from MIS 6 through 4, much of which is best preserved in the archaeological sites fronting the PAP (Marean, 2015; Marean et al., 2014; Wadley, 2015). In the future, we intend to apply to MIS 6 and 4 the same research program described here, but we make some tentative suggestions as to how these glacial phases may have differed or been similar to the LGM. Fig. 5 shows the timeline, changing sea level (Waelbroeck et al., 2002), the distance of the coast from Pinnacle Point (Fisher et al., 2010), a composite speleothem record from the south coast (Bar-Matthews et al., 2010; Braun et al., 2018, 2020 [this issue]), and textual summaries of the interpretations of landscape, habitat and human adaptations discussed below.

MIS 6 is a longer glacial phase than MIS 2 (Jouzel et al., 2007), which includes the LGM. Throughout the approximately 60 kyr of MIS 6, sea levels were predominantly as low as they were for the LGM (Waelbroeck et al., 2002), so for the majority of its time span the PAP was massive (Fisher et al., 2010). We expect that its topography was analogous to the LGM, being largely flat to gently rolling. The geology and soils would have been similar. The broad rivers and streams would have followed similar paths shown for the LGM. The coastline along the southern plains should be analogous to that which we have modeled for the LGM. Therefore,

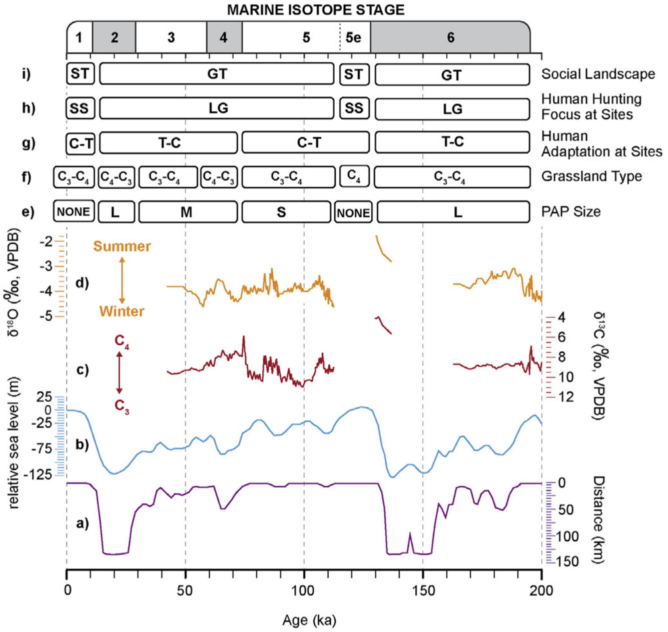

Fig. 5. The changing character of the PAP over the last 200 000 years. A) The distance from Pinnacle Point to the coast (Fisher et al., 2010), B) a relative sea level curve (Waelbroeck et al., 2002), C) the $\delta^{13}C$ from a composite speleothem record, D) $\delta^{18}O$ from a composite speleothem record (Bar-Matthews et al., 2010; Braun et al., 2018, Braun et al., 2020 [this issue]) for C and D, E) the relative size of the PAP (L=large, M=medium, and S=small), F) the predominant grass (C_3 vs. C_4) on the PAP with the dominant grass indicated first, G) the focus of human adaptations at the archaeological sites with C-T = coastal and terrestrial with focus on coast, and T-C = terrestrial and coastal with focus on terrestrial, H) the primary types of animals hunted by humans in the sites with SS = small bodied shrubland species and LG = large bodied grassland species, and I) the social landscape model, with GT = generalized tribal and ST = specialized tribal. E) through to I) are all generalized for this paper.

overall, we expect a landscape structure and habitat zonation similar to that for the LGM. There were short periods of warmer conditions and higher sea levels, for example centered on ~167 ka, when the coast came within ~5 km of Pinnacle Point (Fisher et al., 2010; Marean et al., 2007). At these times, the neo-coastal sites such as PP became once again coastal in character. Such short transgressions would have had devastating consequences for the PAP, disrupting a mature ecosystem, forcing population crashes of plants and animals, almost certainly causing some local extirpations, and driving populations of animals onto the CCL. Human groups must have moved there as well, where they likely came into conflict with residents. In the future, as our records become ever more detailed, it will be exciting to investigate these ecosystem disruptions and use them as case studies to explore how ecosystems crash and reassemble, and how people respond. But for the purposes of this paper we will try to characterize the PAP of MIS 6 as it was during maximum glacial states and lowered sea level, for example at ~150 ka.

During these maximum glacial phases we expect the PAP climate had similar temperatures as the LGM. One of the few archive records of this time is the Pinnacle Point composite speleothem record (Braun et al., 2018). While there is a gap in speleothem formation just before 150 ka, the record before that suggests a mixed C_3–C_4 vegetation trending more C_3. The phytolith record from a Pinnacle Point cave site (PP13B) (Marean et al., 2010) is strangely depleted in grass phytoliths (Albert and Marean, 2012; Esteban et al., 2020 [this issue]), so does not tell us anything about the grass types and suggests a shrubby local habitat. The micromammals at PP30 suggest the local vegetation was shrubby and strongly C_3, probably limestone fynbos similar to today (Matthews et al., 2020 [this issue]; Williams, 2015; Williams et al., 2020 [this issue]). The large mammal faunal assemblages at caves PP13B and PP30 show faunal communities similar to those in the LGM with a dominance of grazing taxa alongside the consistent occurrence of fauna documenting the presence of contemporary CFR shrublands (Rector and Reed, 2010).

The species representation of micromammals from Pinnacle Point cave site PP9 that sample the very end of the MIS 6 is indicative of a grassy habitat, suggesting that within ~2 km of the cave (the foraging radius of owls), grasslands were present. Strontium isotopes of the large grazing ungulates from MIS 6 show that they lived the majority of their lives on the PAP (Copeland et al., 2016), and bulk isotope sampling of these animals shows a mixed C_3 and C_4 grass diet, trending C_3 (Williams et al., 2020 [this issue]). Serial isotope sampling of the southern reedbuck shows a seasonally unchanging mixed C_3 and C_4 diet trending more C_3 (Hodgkins et al., 2020 [this issue]), probably a consequence of a high sedge component in the wetlands associated with the floodplain woodland habitat. All the blue antelope specimens show a pattern similar to the southern reedbuck suggesting they too are not changing their diet much through the year nor migrating. The typically mobile grazers like hartebeest, wildebeest, and bontebok showed a broad range of pattering, with some resembling the southern reedbuck and others showing a pattern of changes in $\delta^{13}C$ that is directional with a broad range (Fig. 4). Overall, the evidence suggests that structurally the central-northern PAP during MIS 6 was similar to the LGM, dominated by shale grassland, floodplain grassland interrupted by patches of shrubland that was most likely dune fynbos-thicket mosaic on calcareous aeolianite. It is likely that more of the grass component was C_3 than during the LGM.

MIS 4 was not as long and cold as either MIS 6 or MIS 2 (Jouzel et al., 2007), nor were sea levels as low (Waelbroeck et al., 2002) (Fig. 5). Where exposed by sea level retreat, MIS 4 topography was similar to the LGM, being largely flat to gently rolling. The geology and soils were similar and the rivers and streams would have followed similar paths as during the LGM, but nowhere did they broaden so dramatically because their southern extent was truncated. Due to the configuration of the PAP, the southern plains exposed during the LGM were absent, and the coastline ran along the southern edge of the northern plains, almost always within foraging distance of hunter-gatherers living in the *neo*-coastal caves and rockshelters at PP and Klasies. This proximity is reflected in that shellfish are present right on through the MIS 4 occupations at these sites. Today the coastline has a strong log-spiral structure where rocky headlands provide reflective coasts with largely quartzite intertidal zones that give way, within the embayments, to sandy beaches and aeolianite or beach rock reefs. In MIS 4, the beaches of the southern plains would not have this structurally controlled log-spiral form, but would have been long straight dissipative sandy beaches interspersed with aeolianite and beach rock reefs. In the area of PP, there would have been nearby estuarine beaches formed by the palaeo-channels of the Gouritz to the west and to the east the Hartenbos and Little Brak and Great Brak rivers (Cawthra et al., 2020a [this issue], 2020b [this issue], 2020c [this issue]).

There are speleothem records from three sites along the coastal margin – Crevice Cave and PP29 at Pinnacle Point, and Herolds Bay Cave (Bar-Matthews et al., 2010; Braun et al., 2018, 2020 [this issue]). All of these records show a shift to stronger C_4 conditions in the carbon isotopes and greater amounts of convective summer rain in the oxygen isotopes from MIS 5 to 4. This result is independently validated by the phytolith record from PP5–6N, where phytoliths show an increase in C_4 with the transition from MIS 5 to 4 (Esteban et al., 2020 [this issue]), as does the $\delta^{13}C$ of ostrich eggshell from Blombos and Klipdrift to the west (Roberts et al., 2016).

Carr et al. (2016) questioned the interpretation of the Crevice Cave record, largely based on their assumption that glacial conditions must bring more winter rain to the south coast, an assumption based largely on qualitative projections of climate patterns. Several empirical records challenge this assumption, including speleothem records (Braun et al., 2017, 2018, 2020 [this issue]), phytolith records (Esteban et al., 2020 [this issue]), and the $\delta^{13}C$ of ostrich eggshell records (Roberts et al., 2016). The LGM regional climate model simulation (Engelbrecht et al., 2019) shows how more rain can come to the coast during glacial conditions. Importantly, these quantitive modeling exercises underscore the need to move from qualitative climate projections to formal climate modeling in Quaternary palaeoscience (Marean et al., 2015).

The best faunal records for MIS 4 are from Klasies River (Klein, 1976, 1983) and Blombos (Henshilwood et al., 2001; Roberts et al., 2016). Both show grassland species, while Klasies shows a stronger grassland pattern and Blombos a stronger shrubland pattern, and in this character, Klasies River is more similar to LGM Nelson Bay Cave. Southern reedbuck is present at all sites, documenting the presence of wetlands and flooded grassland. Wildebeest at Klasies River indicates the presence of short grasslands, most likely associated with clay-rich soils. At Blombos, the large alcelaphine specimens are unfortunately grouped into a combined wildebeest and hartebeest class in publication. Eland are common at both sites, as they are in LGM Nelson Bay Cave, implying the presence of open habitats with available browse. Bushbuck and greater kudu were present but rare in MIS 4 at Klasies – implying thicket - but absent in the MIS 4 at Blombos and LGM at Nelson Bay Cave. Roan are abundant in the LGM at Nelson Bay Cave and missing in MIS 4 from Klasies and Blombos, while quagga was more common in MIS 4 at Klasies than the LGM at Nelson Bay Cave, and very rare in the MIS 4 at Blombos. Springbok is absent from MIS 4 at both Klasies and Blombos, and present in the LGM at Nelson Bay Cave. These differences may be artifacts of sampling, which could disappear as our samples increase, or they may be tracking some specific differences in ecology. Overall, Blombos shows a more shrubland habitat during MIS 4 than Klasies and LGM Nelson Bay Cave, perhaps reflecting a greater component of winter rain. Nevertheless, MIS 4 poses a unique ecological situation – nutritious grassland and productive coastline all within the daily foraging radius of people living in the *neo*-coastal caves and rockshelters. We discuss the implications of this below.

5. Discussion

5.1. Implications for human foraging adaptations

The current archive records for Pleistocene humans along the Cape south coast are well known for their remarkable records of early modern humans in a changing CFR. These sites (Klasies River, Nelson Bay Cave, Pinnacle Point, and Blombos) all currently sit along the coastline, near the intertidal, but during most of their prehistoric occupation humans occupying those sites would have looked out over the PAP (Fisher et al., 2010). We think these prehistoric people focused the majority of their foraging activities on that plain. All the large bodied grazing ungulates that comprised the majority of their terrestrial animal diet require habitats that the PAP provided and the strontium isotopes indicate they were procured from the plain (Copeland et al., 2016). The marine food component of their diet, collected from the intertidal zones (Jerardino and Marean, 2010; Marean, 2014; Marean et al., 2007), most of the time required passage across those plains to reach. The ostrich eggs that supplemented their diet, and were used for the production of flasks, were collected on the plains as well (Hodgkins et al., 2018). Thus, direct archaeological evidence links the lives of the ancient people to the now submerged landscape.

There are good reasons to think that the plains dominated the lives of these ancient people. Fresh water, required daily by humans, was abundant on the plains in the form of rivers and streams (Cawthra et al., 2020b [this issue]) and abundant coastal groundwater seeps (Rishworth et al., 2020 [this issue]). High quality fuel for fires was available on the plains in the woodlands as well as the in the dune fynbos-thicket mosaic of the extensive aeolianites (Cowling et al., 2020 [this issue]), and the populations of large ungulates would have produced large quantities of ungulate dung for fuel for fire. Archaeologists working in the CFR have long recognized the potential significance of the rich diversity of plants for human foragers and those with underground storage organs have been argued to be particularly significant (Deacon, 1984, 1993; Deacon et al., 1986; Marean, 2010; Moffett and Deacon, 1977; Parkington, 1977, 1980). Their remains are sometimes found in Later Stone Age sites (Deacon, 1976; Parkington and Poggenpoel, 1971) and now have been identified in Middle Stone Age (MSA) deposits at Klasies River (Larbey et al., 2019). Experimental studies have begun to provide some information on the CFR edible plant abundance and returns (Botha et al., 2020 [this issue]; De Vynck et al., 2015, 2016b; Singels et al., 2016). All the vegetation types have hotspots that offer good returns but these are seasonally variable, with winter and spring likely to be the better foraging months. For the modern vegetation types on the CCL, plant resources would provide a reliable source of calories albeit probably mostly as a fallback food. Sand fynbos and dune fynbos-thicket mosaic provided the highest returns, and fire consistently increased the foraging returns (Botha et al., 2020 [this issue]). Analogous habitats to some of those on the PAP have not yet been studied, and some may not exist (for example volcanic soils with winter rain). We do not think that any of the PAP vegetation types would have provided plant food returns that significantly exceeded the extant vegetation types. It is important to note that experimental studies show that at least some USO plants would have had lower returns during glacial phases due to impacts of lowered atmospheric CO_2 concentrations on carbon economies (Faltein et al., 2020 [this issue]).

The northern plains, always directly adjacent to these archaeological sites, provided a rich savanna-like habitat with a diversity of grasslands (Fig. 5). We expect short grassland on clay-rich soils, taller grasslands associated with floodplains, and a savanna-like woodland as a perimeter around the floodplains. The increased warm-season rains, relative to the present-day, and rich and varied soils created nutritious rangeland that supported dense and large ungulate populations, particularly to the east. We don't know yet if these supported east-west migrations throughout Pleistocene times when the plain was exposed, but the MIS 6 isotopic evidence from PP30 suggests mixed populations of residents and migrants. On the south coast, bimodal rainfall would have created both cool and warm season growth in the grasses, and this may have supported some resident grazing animals. There may also have been some movement along the drainages, in a north-south direction.

The abundance of rivers and streams offered excellent opportunities for the ambush hunting of large ungulates, and water and wood fuel were plentiful. The fynbos-thicket mosaics associated with extensive patches of calcareous aeolianite would have provided hunting opportunities for bush-habitat game such as bushbuck, grysbok, and bush duiker. The southern plains, a region of predominantly limestone fynbos, was not a particularly rich region for human foragers, though the shrubby fynbos would have provided some small ungulate hunting opportunities and a year-round source of carbohydrates (Botha et al., 2020 [this issue]; De Vynck et al., 2015, 2016b; Singels et al., 2016). The coastline would have provided long dissipative sandy beaches for sand mussel collection, and in areas where aeolianite and beachrock were present, excellent returns under ideal conditions from the intertidal.

For human foragers inhabiting the *neo*-coastal sites, we think the Pleistocene PAP can be grouped into four temporal states based on varying sea level: 1) strong glacials such as MIS 6 and MIS 2 where the southern plains were present and the coastline very distant, 2) weaker glacials such as MIS 4 where the southern plains are absent, the plains are still relatively expansive, and the coastline was distant but still within the daily foraging radius of people, 3) climate phases where sea level was lower than today but where the plain is restricted to a narrow strip along the *neo*-coastline (MIS 5d-a), and 4) interglacials were the PAP is drowned (MIS 5e and the Holocene). Our palaeoscape model for the Holocene suggests that hunter-gatherers living in this environment when the PAP is drowned are hard-pressed to make a living, and on a day to day basis struggle to produce sufficient calories to survive (Wren et al., 2020 [this issue]). This could also apply to the MIS 5d-a stages when the PAP was rather small. We think that the addition of the PAP significantly increased the extent of high quality habitats for hunter-gatherers in the CFR, primarily through the addition of grasslands and woodlands with large populations of large ungulates. MIS 4 likely represents a sweet spot for humans living in the *neo*-coastal sites in that the PAP would be sufficiently large to sustain the resource-rich grassland and woodland ecosystems, and at the same time the coastline is within reach of the hunter-gatherers. From these locations, hunter-gatherers could both exploit the coastline and the grassland habitats. This may explain why there is an increase in human intensity of occupation at PP5-6 during MIS 4 (Karkanas et al., 2015). In the future, we will use our Palaeoscape ABM to explore this hypothesis, and then test it against the archaeological record.

5.2. *Implications for the human social landscape*

A fundamental component of the modern human adaptation is the presence of multi-scale sociality made possible through evolved proclivities to cooperate at high levels with unrelated individuals (Chapais, 2008; Hill et al., 2009). While many animals form local groups or bands that cooperate, only humans form a second social scale of tightly inter-connected bands united by formal gifting and mate exchange (reciprocal exogamy), language, and shared culture. We call these ethno-linguistic groups and/or tribes (Marlowe, 2005). This is a uniquely human trait and its time and place of origin is a focus for much research. While some models propose that multi-scale sociality evolved early, perhaps with the first major hominin encephalization (Hrdy, 2011, 2014; Wilson, 2012), others propose a late evolution during the late Middle or Upper Pleistocene associated with the evolution of the modern human lineage (Ambrose, 2010; Ambrose and Lorenz, 1990; Marean, 2014, 2015, 2016). By the Holocene, when the PAP was submerged, geographically small and economically specialized tribes existed on the south coast (Sealy, 2006). The cluster of sites along the south coast provide an ideal database to investigate the "late origin" model, and here we discuss the implications of our reconstruction of the PAP ecosystem for this active research question.

What was the potential social landscape on the PAP during the glacial states discussed above? Marlowe (2005) has summarized the ethnographic data on typical sizes of hunter-gatherer local groups (bands) and ethno-linguistic groups (tribes). Bands (mean population size = 47) use about 1600 km^2 while tribes (mean population size = 1749) use about 37845 km^2. Variance in group size is large, and coastal hunter-gatherers are known to have smaller ranges and denser population sizes than terrestrial hunter-gatherers. Despite these caveats, the PAP at maximum size would likely support one tribe, maybe two, made up of a number of bands. Hunter-gatherer tribes normally organize themselves along resource-use and natural boundaries aligned to dividing features on the landscape, such as mountain chains and rivers. This is well illustrated in the ethnographic literature where there are good maps of tribal boundaries and knowledge of resource use. Examples include the tribal boundary structure found at the time of first European contact of the Australian aborigines (Tindale, 1974), the California Indians (Kroeber, 1925, 1939), and the Indians of Tierra del Fuego (Furlong, 1917; Lothrop, 1928).

Two possible tribal structures seem reasonable for the PAP. The PAP could have been inhabited by a single tribe with band ranges encompassing the interfluves (= generalized tribe PAP model). This would provide bands with a wide range of resources including Cape flora and fauna (the CCL to the north), grassland (the PAP northern zones), floodplain grassland (throughout the PAP), woodland (the PAP northern zones), coastal Cape flora and fauna (the southern PAP), and coastline (far south). Alternatively, there could have been a tribal division into coastal and terrestrial PAP resources, with one tribe focused on the coast and another the PAP interior (= specialized tribe PAP model). This structure was observed at colonial contact where resource-rich coastlines were present (i.e. Australia, California, and Tierra del Fuego). With the "specialized tribe PAP", one tribal adaptation would be coastally focused and largely restricted to the limestone fynbos region, and one would be plains-focused and not have access to coastal resources.

These two alternative social landscape structures represent ends of a continuum, and we think it likely that the human social landscape may have been temporally dynamic in response to the changing structure of the PAP and, with the Holocene condition being the only one preserved at contact, and revealed in the Holocene archaeology (Sealy, 2006). We provide a simplified proposal as to the evolutionary development of the PAP and human adaptations and the social landscape in the CFR (Fig. 5). The Holocene was a uniquely stable phase of climate through the late Quaternary, and Pleistocene cold phases were particularly variable (Ditlevsen et al., 1996, 2005, 2017; Rehfeld et al., 2018). Marean et al. (2014) argued this would have had significant impacts on the nature of Pleistocene versus Holocene human adaptations. Holocene stability offered a context for population growth, increasing economic specialization, and fragmentation into small and specialized tribal units of the type observed at contact in Australia, California, and Tierra del Fuego.

During periods of sea level regression and the ongoing exposure of the PAP, as low density human populations expanded on to the PAP, we expect that a generalized tribe structure existed, with bands inhabiting the interfluves and exploiting the resource base broadly. Tribal groups had a broad resource base maintained through diverse habitat access, low population densities, and larger tribal areas. The geographic range of ethno-linguistic groups and bands was larger than is typical in the Holocene and historic ethnolinguistic records, perhaps much larger. We expect people would have been highly mobile, perhaps far exceeding that typical for the Holocene. Regular Pleistocene climatic instability provided constant turnover in the habitats and a regular check on population growth, economic specialization, and the division of groups into small and specialized tribal units. Coastal habitats may have been subject to regular disruption if sea level was changing regularly in reaction to this climatic instability. Sea level transgressions would have disrupted social landscapes, immediately displacing the coastal groups. The sea level model suggests that most Pleistocene transgressions experienced rapid loss of land (Fisher et al., 2010), due to the gradual slope of the PAP. Given the wildly fluctuating Pleistocene climate, this cycle of maturation and destruction of the

PAP and its downstream impact on the human social landscape was a defining feature of the Pleistocene CFR (Marean et al., 2014), and may have been for Africa more generally.

When sea levels reached a point of stability during MIS 4, it seems likely that a “generalized tribe PAP” structure would have existed. At this time, the PAP was insufficiently large to allow the maintenance of two separate tribes following separate economies since the plains were narrow. Furthermore, archaeological records at Klasies, Pinnacle Point, and Blombos, show the exploitation of both shellfish and plains animals, indicating that humans could readily exploit both the coast and the plains. We also observe long high-intensity occupations of the archaeological sites during this period, where the humans could blend resource use among hunting large game on the plains, small game hunting in the shrublands and thickets of the CCL and PAP dunescapes, collection of shellfish on the coast, and plant food gathering in diverse habitats. These times, when the plains and the coast and the Cape shrublands are available, which would have occurred throughout MIS 5d-a, but reached a peak of productivity in MIS 4, can be viewed as sweet-spot periods that are regularly overturned by sea level rise. Faith (2011: 226) argued that “[r]ich Pleistocene ungulate communities with elevated biomass could have favored a MSA foraging niche geared toward the exploitation of terrestrial herbivores”. We agree that the PAP provided these ungulate communities, and their loss was catastrophic. However, we think the MSA foraging niche in the CFR was one that triangulated between: 1) the rich foraging returns offered by the coast, that under peak conditions can exceed the top large mammal hunting returns (De Vynck et al., 2016a), 2) large mammal exploitation that mixed grassland, woodland, shrubland and thicket hunting, and 3) a plant gathering strategy that exploited the diversity and abundance (albeit patchily) of a year-round carbohydrate resource associated with the diversity of biomes represented on the contemporary coastline and adjacent PAP (De Vynck et al., 2015, 2016b; Singels et al., 2016). The biggest change in human adaptation in the CFR occurred at the Pleistocene-Holocene boundary, where the PAP was lost and this “sweet-spot” foraging system was gone.

Wren et al. (2020 [this issue]) show us that removing the PAP and its resources from the CFR resource base results in a challenging foraging situation where the forager is hard-pressed to provide sufficient calories. The Holocene archaeological record in the CFR documents a dramatic increase in the range of food resources taken (Clark and Kandel, 2013; Deacon, 1984; Marean et al., 2014) and regular signs that some resources are being over-exploited (Klein and Steele, 2013). Under the stable climatic conditions of the Holocene, rising human populations in this resource-poor environment would have resulted in a highly specialized social landscape where tribal groups focused intensively on their local resource base, specialized their adaptation around it, and defended its boundaries. This social landscape on the south coast was vividly captured in the study of Sealy (2006).

6. Conclusions

At the height of its geographic extent, during strong glacial climates, the PAP added a landmass the size of Ireland to the CFR. During strong interglacial climates, the PAP was submerged and its component ecosystems either disappeared entirely, or shrank to small and fragmented slivers along the steeply rising contemporary coastline. The lower sea levels of the Pleistocene glacial periods exposed the PAP to varying degrees, and the dynamic PAP was a significant factor in the diversification of the mega-diverse CFR biota (Grobler et al., 2020 [this issue]). Numerous lines of evidence suggest that the PAP was of extraordinary importance to early modern humans in coastal South Africa where is found one of the richest records for modern human origins.

The PAP differed markedly from the contemporary coastal foreland of the southern CFR in terms of its physiographic features and component ecosystems: 1) it was flat, 2) it had large meandering rivers and streams draining from the interior to the coast, 3) it had abundant fresh water in these rivers and streams as well as seeps, 4) it was more fertile than the interior of the CFR, 5) the coast was dominated by long sandy beaches and lacked the rocky reef and cliff coasts common on the CCL, 6) it had expansive and fertile, well-watered grasslands, 7) the grasslands supported large and diverse grazing ungulates that had both resident and mobile populations, 8) woodlands were extensive along the floodplain perimeters, and 9) the woodlands were inhabited by a rich woodland fauna including giraffe.

The PAP provided a rich foraging habitat for Pleistocene modern humans living in the well-known archaeological sites along the current *neo*-coastline and was the deciding factor separating Pleistocene from Holocene modern human adaptations in the CFR. The Pleistocene modern human adaptation captured in the *neo*-coastal sites was oriented around a resource base that triangulated coastal resource use, large mammal hunting in diverse habitats, and plant food collection. Interglacial sea level rise disrupted these systems, causing widespread collapse in the ecological and social landscape, which would then stabilize when sea level change stopped. While the Holocene and contact period may represent our clearest model of human and ecological conditions in the CFR region, it is in fact the outlier.

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