

Vertebrate Paleobiology and Paleoanthropology Series



Sacha C. Jones
Brian A. Stewart *Editors*

Africa from MIS 6-2

Population Dynamics
and Paleoenvironments

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Vertebrate Paleobiology and Paleoanthropology Series

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ISSN 1877-9077 ISSN 1877-9085 (electronic)
Vertebrate Paleobiology and Paleoanthropology Series
ISBN 978-94-017-7519-9 ISBN 978-94-017-7520-5 (eBook)
DOI 10.1007/978-94-017-7520-5

Library of Congress Control Number: 2015957232

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Cover illustration: Cover image created by Katherine Clahassey.

Printed on acid-free paper

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The registered company is Springer Science+Business Media B.V. Dordrecht

Preface

Africa, from Marine Isotope Stages (MIS) 6 to 2, approximately 190–12 ka (thousand years ago), witnessed our species' biological development and behavioral florescence. To date, archaeological, paleontological, and genetic research on this period has been dominated by efforts to classify “modernity” and chart the geographic spread of *Homo sapiens* out of Africa. While such themes remain important, reconstruction and explanation of the demographic processes that occurred within Africa from MIS 6-2 are issues that are consistently under-addressed. This is a major drawback given that population dynamics within Africa played a central role in our species' genetic and cultural evolutionary trajectories. Genetic analyses suggest that African populations experienced multiple bottlenecks over the last 200 ka, interspersed with population expansions (releases). The former almost certainly engendered population isolations, extinctions, genetic and cultural drift, and biological and behavioral adaptation; while the latter saw humans radiate and colonize, with some groups eventually dispersing from, and re-entering, the continent. Analogously, recent theoretical advances in cultural evolution suggest that demography was perhaps the single most important factor underlying modern human innovation.

Yet until these insights can be contextualized, dated, and elaborated using the increasingly refined archaeological and paleoenvironmental records for late Middle and Late Pleistocene Africa, they remain mere glimpses of the complex paleodemographic processes that made us what we are today. To begin redressing this problem, we held a conference at the McDonald Institute for Archaeological Research, University of Cambridge in July 2010, entitled *Africa from Stages 6 to 2: population dynamics and paleoenvironments*. This conference was a first attempt to explore the potential of using diverse African datasets—archaeological, paleoenvironmental, paleontological, and genetic—to reconstruct spatiotemporal population histories during MIS 6-2. The principal aim was to investigate continent-wide population dynamics during MIS 6-2 by fostering interdisciplinary discourse between experts working in ecologically comparable zones across Africa. Twenty-three leading researchers in African archaeology, paleoenvironments as well as genetics and paleontology were thus invited to present their work at the conference. The main issues that were raised included: (1) the impact of this glacial-interglacial-glacial cycle on human group sizes, movements, and distributions throughout the continent; (2) the macroevolutionary and microevolutionary processes underpinning our species' anatomical and behavioral evolution; (3) an initial assessment of the state of the relevant data for addressing these issues and; (4) setting an agenda whereby Africa can benefit from, and eventually contribute to, the increasingly sophisticated theoretical and methodological paleodemographic frameworks developed on other continents.

The scope of the conference was pan-continental. This was not because we expected to pin down population dynamics on this grand scale, but rather because we hoped to address three further objectives: (1) to encourage a more balanced geographical coverage than is typical in MSA/early LSA research (wherein eastern and southern Africa are focal points); (2) to facilitate trans-continental comparisons in order to evaluate the current status of the data; and (3) to foster discourse among and between researchers working in different regions and biomes of Africa. The conference was thus organized according to the biome in which the research was taking place, rather than according to a specific region or time period. This organization—wherein research results from the Kalahari, for example, were presented alongside those from the Sahara, or those from highland Lesotho discussed in relation to highland Ethiopia—proved fruitful. This book, therefore, is similarly organized according to the broad ecological zone into which the different authors' research falls. We have subdivided the papers into: (1) coasts; (2) deserts; and (3) grasslands, woodlands and rainforests. In addition to papers focusing on regional African archaeological and palaeoenvironmental records, we also include two broader scale papers by researchers with expertise in physical anthropology and genetics. This multidisciplinary breadth is essential for addressing questions regarding palaeodemography. In the final chapter of the book, Peter Mitchell raises a number of important theoretical issues and addresses how we can begin to model past population dynamics in Africa from MIS 6-2.

Scholarship on Africa has previously lagged behind that of other continents, particularly Europe, in generating models of prehistoric population dynamics that can be tested against high resolution archaeological and paleoenvironmental records. There are many reasons why this is so, some of which have clearly influenced the composition of this book. First, archaeological and paleoenvironmental research coverage on this enormous continent is extremely patchy, dictated by a host of factors including the variable preservation and exposure of ancient remains, differing research traditions and recurrent political instability. The prehistoric records of some areas (e.g., East, North, and southern Africa) are more thoroughly researched, and thus more highly resolved, than others (e.g., central and West Africa), making our chapter balance inevitably, and regrettably, skewed toward the former. A related reason for Africa's dearth of paleodemographic research compared to other continents is the relative paucity of African researchers working on MIS 6-2. Instead, most research teams and funds come from international institutions with geographically circumscribed research foci instead of trans-regional comparative aims or inter-project collaborations. Particularly rare in research on MIS 6-2 are black African scientists, who have generally tended to concentrate more on earlier (Plio-Pleistocene) or later (Holocene) periods of their continent's past. The result is another unavoidable imbalance in this book. By taking a pan-continental, trans-regional approach to the population dynamics of prehistoric Africans, however, we hope this book will inspire researchers in Africa to investigate MIS 6-2 not only in the continent's best researched regions and archaeologically more remote corners, but also, crucially, in the areas connecting these two extremes. For paleodemographic research in Africa, it is still early days. This book, while perhaps raising more questions than providing answers, takes a critical first step toward elucidating the demographic processes that underpinned our species' development during this formative evolutionary phase.

The *Africa from Stages 6 to 2: population dynamics and paleoenvironments* conference was generously funded by the D.M. McDonald Grants and Awards Fund at the McDonald Institute for Archaeological Research at the University of Cambridge. We are sincerely grateful to the McDonald Institute for funding the conference. This three-day event was also sponsored by the Centre of African Studies at the University of Cambridge. We thank the speakers who presented their research at the conference, most of whom have contributed to this volume, as well as the conference's attendees, who contributed to stimulating, important discussions on the topics raised in this book. We are grateful to Katherine Clahassey of the University of Michigan's Museum of Anthropological Archaeology for skillfully creating the cover illustration. Finally, we dearly thank all those who have supported the creation of this book and who have been instrumental in its completion. First, we are grateful to Springer's Series Editors, Eric Delson and Eric Sargis, for their commitment, help and support throughout all stages of this volume's development. We thank all fifty-two peer-reviewers for their comments on the book's chapters. Last but not least, we are indebted to all the chapter authors who have contributed so generously to this volume. We are most grateful for their time and patience and we sincerely hope that they will enjoy being part of this book.

Sacha C. Jones
Brian A. Stewart

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Chapter 1

Africa from MIS 6-2: The Florescence of Modern Humans

Brian A. Stewart and Sacha C. Jones

Abstract Africa from Marine Isotope Stages (MIS) 6-2 saw the crystallization of long-term evolutionary processes that culminated in our species' anatomical form, behavioral florescence, and global dispersion. Over this ~200 kyr period, Africa experienced environmental changes on a variety of spatiotemporal scales, from the long-term disappearance of whole deserts and forests to much higher frequency, localized shifts. The archaeological, fossil, and genetic records increasingly suggest that environmental variability profoundly affected early human population sizes, densities, interconnectedness, and distribution across the African landscape – that is, population dynamics. At the same time, recent advances in anthropological theory predict that such paleodemographic changes were central to structuring the very records we are attempting to comprehend. The book introduced by this chapter represents a first concerted effort to assess modern human population dynamics throughout Africa, whether these changed with environmental fluctuations, and how they contributed to our species' evolutionary trajectory.

Keywords Cultural transmission • Human evolution • Middle and Late Pleistocene • Middle and Later Stone Age • Paleodemography • Paleoenvironment • Population dynamics

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Introduction

The last three decades represent a watershed in our understanding of modern human origins. In the mid-1980s, evolutionary genetics established that the most ancient human lineages are African (Cann 1988; Vigilant et al. 1991). Since then, steady streams of genetic, paleontological and archaeological insights have converged into a torrent of evidence that Africa is our species' evolutionary home, both biological and behavioral. When these changes occurred, however, remains less well understood, and much less so how and why. Where within Africa modern humans and our suite of behaviors developed is also problematic. One thing seems clear: the changes that shaped our species and its behavioral repertoire were gradual, rooted deeper in the Pleistocene than previously imagined. Anatomically, the accrual of modern traits and disappearance of those deemed archaic now appears to have been a phased process lasting some 400 kyr (Grine 2016; Lahr and Foley 2016), a biological blurring underscored by genetic evidence for later admixture with archaic forms outside (Green et al. 2010; Reich et al. 2010) as well as inside (Hammer et al. 2011; Mendez et al. 2013) the continent (but see Eriksson and Manica 2012). Similarly, the pedigrees of many complex behaviors – including hafting (~500 ka; Wilkins et al. 2012; Barham 2013), projectile technologies (~279 ka; Sahle et al. 2013), and pigment use (~270 ka; Barham 1998, 2002a) – seem to attenuate with nearly every year that passes.

Yet it is not until 200 ka – roughly the start of Marine Isotope Stage (MIS) 6 – that the first fully derived modern human anatomical features appear (McDougall et al. 2005). We must wait another 100 kyr, until late MIS 5, for the first compelling archaeological expressions of behaviors characteristic of living people, including external symbolic storage (e.g., Bouzouggat et al. 2007; Henshilwood et al. 2009). Thus Africa from MIS 6-2 seems to have witnessed the crystallization of complex, longer term evolutionary processes set in motion at or beyond the advent of Middle Stone Age

(MSA) technologies ~300 ka (McBrearty and Brooks 2000; McBrearty 2007) or possibly earlier (cf. Wilkins et al. 2012). How and why this happened at this particular time are challenging questions indeed, involving constellations of interconnected variables that are difficult to parse. With recently accelerated research on this topic, however, important variables are being successfully isolated. Of particular significance are population dynamics and their relationship to paleoenvironments, and how both changed through time and space.

Population Dynamics and Paleoenvironments

The end of the Pleistocene epoch witnessed increasingly volatile climates with major implications for changes to African environments and their resource structures. Globally, MIS 6-2 saw a particularly warm interglacial period (MIS 5, but particularly 5e) bookended by some of the Pleistocene's most severe glacials (MIS 6, 4 and 2), with an intervening stage (MIS 3) so erratic that researchers disagree over which category it should fall into (Fig. 1.1). Humans in Africa were faced with immense changes in humidity, temperature, windspeeds, vegetation, animal biomass and landscape geomorphology that occurred at a variety of spatiotemporal scales, from the long-term disappearance of whole deserts to much higher frequency, localized shifts that were perceptible to people over the course of their own lifetimes. The human responses to these pressures were undoubtedly as diverse and complex as the changes themselves, engendering a wide range of biological and cultural selective outcomes. As with all humans, but particularly with hunter-gatherers due to their subsistence practices, local and regional shifts in resource base have demographic consequences and affect, for example, population sizes, densities, interconnectedness and distribution across the landscape – that is, population dynamics. Changes in human population dynamics – often but of course not exclusively initiated by environmental change – can be seen as part of a suite of adaptive tools that were mediated by, and in turn influenced, human biological and cultural evolution and history.

The evidence for widespread and rapid paleoenvironmental changes through late Middle and Late Pleistocene Africa that has accumulated over the past three decades has rendered major population flux over this period probable (e.g., Blome et al. 2012). Crucially, this has recently begun to be confirmed by numerous evolutionary genetic studies of modern African populations throughout the continent (Tishkoff et al. 2009; Henn et al. 2011; Soares et al. 2016). Such data are particularly significant in light of recent insights from cultural evolutionary theory that suggest effective population size influences rates at which innovations are

generated and transmitted (e.g., Powell et al. 2009; Collard et al. 2013). Thus paleodemography may have a direct bearing on how we interpret the behavioral evolution of our species, particularly the wax and wane of complex expressions seen most famously in the Still Bay and Howiesons Poort of southern Africa (Henshilwood and Dubreuil 2011). Such expressions seem to surface only intermittently throughout MIS 6-2, before culminating explosively in the relative climatic stability of the Holocene. The implications of this argument, though enticing, are extremely contentious not least because inferring information about metapopulation size from archaeological data is often problematic (see Chamberlain 2006). Beyond this specific issue, however, the weight of genetic, paleoenvironmental, fossil, and archaeological evidence is making it increasingly clear that the stability of African populations from MIS 6-2 vacillated. Any understanding of modern human origins and early history is therefore contingent upon the exploration of African population histories.

While timely, the topic of Africa's demographic history is far from new. From its outset until relatively recently, African prehistory was cast within a culture historic framework in which archaeological changes were explained with reference to unfounded assumptions about successive waves of incoming populations (Robertshaw 1990; Mackay 2016). Beginning around the mid 20th century, attempts were made to more explicitly relate hypothetical population dynamics to climatic changes (Clark 1959, 1960; Lee 1963), the latter as postulated in the subsequently disproven pluvial-interpluvial schema (e.g., Brooks 1914; Wayland 1934; Leakey 1951). With characteristic incisiveness, John Desmond Clark (1959, 1960) provided the most penetrating treatment. Seeking to explain gross patterns of spatiotemporal variability in the African paleoanthropological record, Clark invoked climate shifts and their impact on human population dynamics against a background of longer term, macroevolutionary trends in human cognition and technical skill. He hypothesized that important changes were ushered in with the MSA, when behavioral advancements allowed regionally distinct technologies to develop during wet 'pluvial' periods as populations became isolated and adapted their toolkits to varying ecologies. Punctuating these phases of prolonged stasis and diversification were shorter and drier 'interpluvials', which provoked rapid cultural change ("speed-up") stemming from enhanced innovation and population dynamism. Clark (1960: 310) wrote that during such times,

“...decreasing rainfall may be expected to have opened corridors and sometimes highways from north to south and from east to west, which seem to have invited, even though they also sometimes sidetracked, movement by groups forced to migrate by the deterioration of their traditional environment. Sometimes biological proof, in the shape of human fossils, confirms this. At other times we have to rely on different evidence, for example

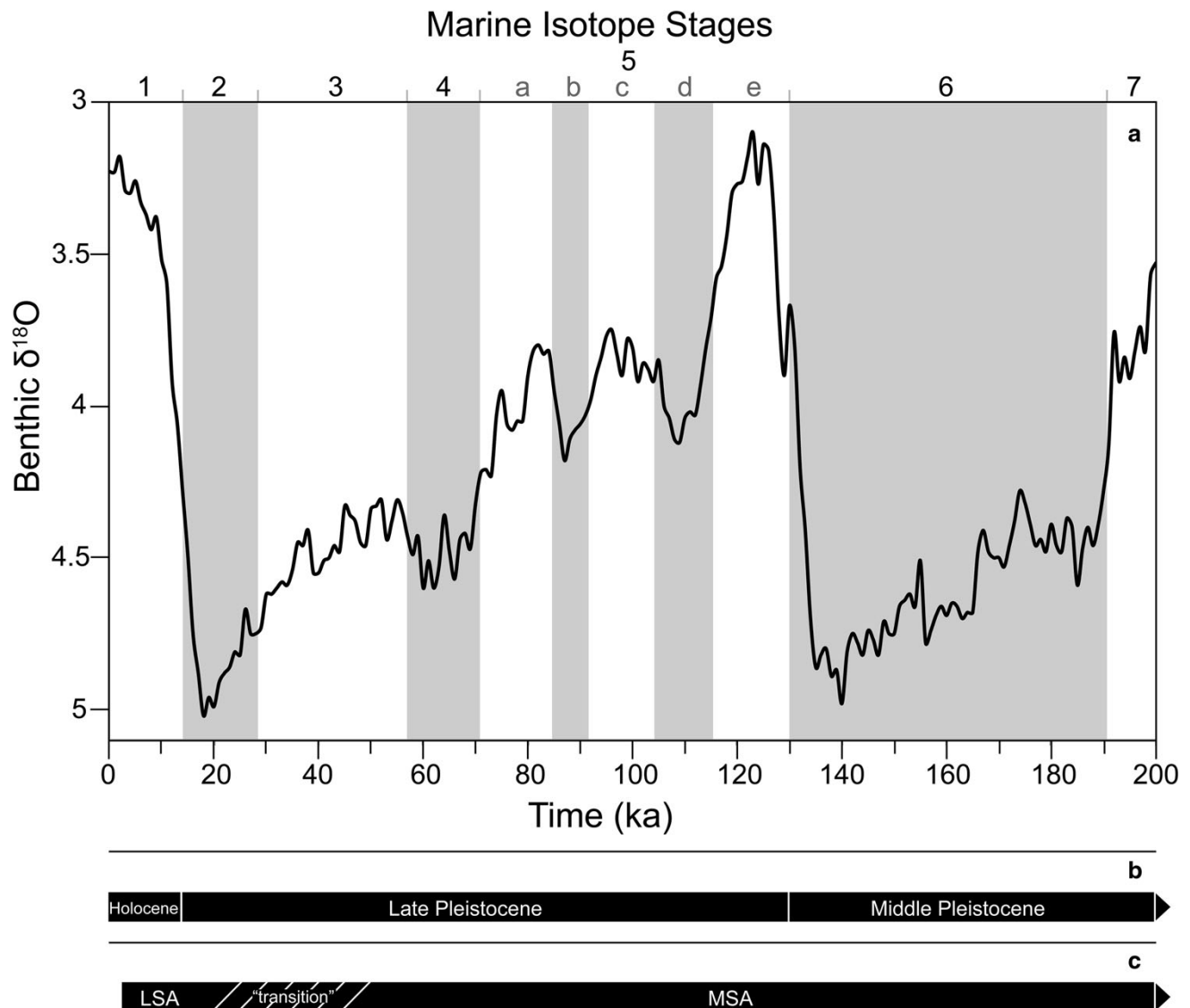


Fig. 1.1 Climatic, geological, and cultural frameworks used in this chapter and book. **a** Marine Isotope Stages (MIS) 6-2 (191–14 ka) differentiated according to Lisiecki and Raymo's (2005) LR04 stack, an average record of global benthic $\delta^{18}\text{O}$ measuring global ice volume and deep ocean temperature; MIS 6: 191–130 ka; MIS 5: 130–71 ka; MIS

4: 71–57 ka; MIS 3: 57–29 ka; MIS 2: 29–14 ka. **b** Geological ages (Middle and Late Pleistocene) and epoch (Holocene) correlating to MIS 6-2. **c** Major divisions of the African Stone Age archaeological record correlating to MIS 6-2; *MSA* Middle Stone Age; *LSA* Later Stone Age

the patterns of spread of new items of cultural equipment. Contact between bands naturally encourages the spread of cultural traits, and new inventions or techniques may be surmised to have been speedily transmitted at times of ecological change and population movement."

Clark's observations – though predicated on a flawed climatic model, lacking a chronological framework and inherently speculative – were nonetheless prescient. Interpreting MSA diversification, the pace of behavioral evolution, the role of climatic fluctuations on population dynamics and cultural transmission, the opening and closing of biogeographical corridors and barriers, the meaning of similar

yet widely dispersed artifact forms and human fossils, remain as resonant today as they were a half-century ago. What is fundamentally different about today are the data. In 1960, Clark listed six datasets "essential to any study of the life of early man, if the results are to have lasting value" (Clark 1960: 307). These were: (1) a chronological framework; improved knowledge of (2) artifact typologies and (3) the spatial distributions of stone tool industries; (4) improved paleoenvironmental data and its incorporation into paleoanthropology through interdisciplinary collaboration; (5) careful site selection and excavation; and (6) the appropriate use of ethnography. In the succeeding half-century,

massive strides have been made toward each, with the ongoing construction of a chronometric framework for Middle and Late Pleistocene Africa arguably the most significant development (e.g., Schwarcz 2001; Jacobs et al. 2008; Bouzouggar and Barton 2012; Cochrane et al. 2013). Another dataset worthy of Clark's list – albeit one the importance of which he could not have known in 1960 – is genetic evidence from extant Africans and the fascinating insights they are offering into the evolutionary history and phylogeography of modern human lineages. We must remember, however, that while these data generate important questions that can usefully guide archaeological research – providing what Cornelissen (2016: 301) calls “an enriched context” – they lack historical detail and chronological resolution. As Van Peer (2016: 157) notes, “it is archaeology's role to critically develop models based on genetic diversity patterns into historic and explanatory scenarios.”

Structure of the Book: Why Biomes?

At 12 million square miles (30 million km²), Africa covers some 20% of earth's total land surface and is the world's second largest continent. Unlike any other, its landmass is distributed fairly evenly across the Equator, reaching ~35° latitude both north and south. The upshot is a ‘sandwich’ configuration, with mirrored rainforest to woodland to savanna to desert to Mediterranean littoral environments as one moves from the Equator north or south (Barham and Mitchell 2008). This broad ecological symmetry presents unique opportunities for interhemisphere comparisons of paleoenvironmental shifts, and resulting adaptive behaviors of early modern human groups operating in different yet ecologically comparable areas of the continent. This is particularly interesting with respect to mounting evidence for the asynchronous nature of environmental change in North *versus* sub-Saharan Africa, as it implies that at certain times what are today similar environments either side of the Equator presented humans with very different conditions. Because of its size and colonial history, however, the study of Africa's past has traditionally been pursued in different areas with relatively minimal inter-regional communication. While this problem is more acute for Africa's recent archaeology, deeper periods including MIS 6-2 are also affected, most notably by the conventional division between North and sub-Saharan Africa but also by that between largely francophone West/Central and anglophone northeast, East and southern Africa.

For all these reasons, we have organized the book, like the 2010 Cambridge conference from which it derives, according to biome rather than by region. Here we use biome in its original sense as referring to large-scale

ecosystem units with similar biotic structure and macroclimate (e.g., deserts, rainforests etc.), rather than as a proxy term for subordinate, geographically specific units such as ecoregions (e.g., Nama-Karoo semi-desert, Guineo-Congolian lowland rainforest etc.). At the conference, papers were subdivided into sessions on coasts, deserts, highlands, savannas and mixed woodlands, and rainforests. This structure helped facilitate inter-regional comparisons and the exchange of ideas between researchers working on similar issues in distant parts of Africa. Attendees felt that this was one of the meeting's main strengths and we have therefore retained it here. However, for the book we collapse the biomes into three sections: (1) coasts; (2) deserts; and (3) grasslands, woodlands, and rainforests. In addition to these sections with chapters detailing regional archaeological and paleoenvironmental records, we include a section dedicated to wider perspectives with more synthetic chapters by experts in genetics (Soares et al. 2016) and human paleontology (Grine 2016). This multidisciplinary breadth is essential for any successful treatment of such a complex topic. In the final chapter of the book, Mitchell (2016) traces key themes raised throughout, and discusses future prospects and challenges for reconstructing African population dynamics and paleoenvironments from MIS 6-2.

Coasts

Extending for ~30,000 km excluding Madagascar (Orme 2005: 9), Africa's coastline is surrounded by the Atlantic and Indian oceans and the Mediterranean and Red seas. The lower reaches of some of Africa's major rivers dissect this coastline (e.g., the Congo and the Zambezi), with some creating complex deltaic environments (e.g., the Nile and the Niger). A diversity of coastal ecologies exists along Africa's littoral, dictated by varying latitudes, regional geographies and climatic regimes, with vegetation varying from one extreme (e.g., desert) to another (e.g., tropical rainforest). For example, Mediterranean vegetation biomes are found at the extreme north and south of the continent, with mangrove habitats along West and East Africa. Coastal zones commonly consist of complex ecotonal and mosaic habitats, in places alternating between desert, subdesert steppe, savanna grasslands and woodland, and lowland tropical forest. Fluctuations in Pleistocene sea level resulted in variable exposure of Africa's continental shelf; for example, sea-level lowstands would have exposed little land in northeast Libya (Jones et al. 2016) yet extensive areas in southern Africa (van Andel 1989; Fischer 2010; Dewar and Stewart 2016), particularly in the area of the Agulhas Bank (Carr et al. 2016). Relative to other large continents, however, Africa's continental shelf is narrow, averaging only 25 km in width (Orme 2005: 9).

Uniting the chapters on coastal records from MIS 6-2 is the relationship between coastal habitats and human occupation with respect to three issues: behavioral complexity, coasts as refugia, and coasts as dispersal corridors. The archaeological records of coastal sites in the Maghreb of northwest Africa and South Africa are well known for exhibiting at least relatively brief periods of seemingly enhanced behavioral complexity (e.g., shell beads, osseous technologies, and engraved ochre, bone and ostrich eggshell). This was particularly the case during late MIS 5 and MIS 4 in Aterian, Still Bay and Howiesons Poort contexts (e.g., Henshilwood et al. 2002; d’Errico et al. 2005, 2008, 2009; Bouzouggar et al. 2007; Texier et al. 2010), but also in earlier MSA contexts in mid-MIS 5 (~100 ka) at Blombos Cave (Henshilwood et al. 2009, 2011) and mid-MIS 6 (~164 ka) at Pinnacle Point 13B (Marean et al. 2007; Brown et al. 2009), both coastal caves along South Africa’s southern Cape. The spatiotemporal distribution of these so-called cultural indicators of behavioral complexity seems to suggest they are more frequently associated with coastal or near-coastal settings, and are more common from late MIS 5. Robbins et al. (2016), for example, note that comparable innovations have yet to be found in similarly early MSA contexts in the Kalahari. Findings from the southern Cape coast have been the basis of arguments that link shellfish exploitation with behavioral complexity and the evolution of modern human cognition, where the southern extremity of Africa is central to these evolutionary developments. Parkington (2001, 2003, 2006, 2010) has suggested that regular shellfish consumption contributed to encephalization, through the benefits of a diet rich in omega-3 long-chain polyunsaturated fatty acids. Encephalization resulting from this dietary shift perhaps enabled various innovations that we currently associate with ‘behavioral modernity’. In contrast, Marean suggests that humans were able to exploit this new dietary resource as a consequence of modern human cognition. Given the earliest evidence for shellfish exploitation c.164 ka at Pinnacle Point 13B, and for other advanced behaviors of a comparable age (e.g., ochre use, heat treatment of rock for tool manufacture), he argues that modern human cognition was coincidental with the origin of *Homo sapiens*, rather than there being a decoupling of anatomical and cognitive modernity (Marean et al. 2007; Marean 2010, 2011, 2014). Both Parkington and Marean see the south coast of South Africa as playing a central role in the origins of our species (Parkington 2010; see also Compton 2011), with the region’s plant diversity, resource-rich coastline and moderate climate all providing “the ideal conditions for a refuge for the bottlenecked modern human lineage during the long cold MIS6” (Marean 2011: 434).

Both this MIS 6 southern Cape refugium scenario (Wurz 2013; Lombard et al. 2013) and the importance of South Africa in species origins models (Lahr and Foley 2016) have

nevertheless been questioned. Two issues are of particular importance. The first of these touches on a greatly debated subject: are we looking at behavioral (or cognitive) complexity in the right way, or are we constrained by our own assumptions? Perhaps diversity in MSA lithic reduction strategies (Jones et al. 2016; Mackay 2016; Van Peer 2016) is a viable measure of behavioral complexity, reflecting modern cognitive capacities for finding adaptive solutions to ecological, social, and demographic changes. Perhaps, stone artifacts – the most abundant material remains available to us – are somewhat overlooked in favor of more obvious yet less frequent signs of behavioral complexity (e.g., pierced shells, engraved ochre etc.). An absence of evidence is not necessarily evidence for the absence of cognitively complex populations, particularly when our understanding is hampered by a severe dearth of certain datasets, such as the intangible (e.g., body decoration) and unpreserved (e.g., wood and hide). It is important to continue challenging how we define and think about behavioral and cognitive complexity (e.g., Shea 2011; Wadley 2013), and to acknowledge and assess the biases in our records.

This brings us to the second question: could these patterns simply reflect a geographic sampling bias, created by an intense research focus on certain regions – the Maghreb and South African coasts – driven in part by coastal geomorphologies where mountainous areas rich in caves and rockshelters are situated close to the coast? Like the chapters in this volume, most studies of ancient African coastal occupation and human exploitation of marine resources focus almost exclusively on the far north and south, which together constitute a tiny proportion of Africa’s vast coastline (e.g., Volman 1978; Walter et al. 2000; Erlandson 2001; Parkington 2003, 2010; Klein et al. 2004; Marean et al. 2007; Avery 2008; Dewar 2008; Steele and Klein 2008; Ramos et al. 2008; Jerardino and Marean 2010, 2011, 2014; Sealy and Galimberti 2011; Steele and Álvarez-Fernández 2011; Dewar and Stewart 2012; Langejans et al. 2012; Dusseldorp and Langejans 2013; Will 2013; Kyriacou et al. 2015). As fascinating as these records are, this geographic bias inevitably contracts our view of African coastal adaptations in prehistory. An intriguing prospect would be to discern how the MIS 6-2 records of the coastal habitats discussed in this volume contrast with those of Africa’s non-Mediterranean shorelines (e.g., coastal rainforests, mangroves, deserts, steppes, savannas etc.). For example, how do different African coastal habitats compare in terms of incidences of marine resource exploitation, archaeological expressions of behavioral complexity, past population dynamics, and the extent to which each was interlinked or disconnected in the past? Neither do we have sufficiently representative coastal records even in southern and North Africa. Sealy (2016), for example, points out that sample size may be a notable problem, with more records dating to

MIS 6 needed in order to discern if anatomical and behavioral modernity were decoupled. Similarly, our ability to address questions of past population dynamics in southern Africa, one of the continent's better-studied regions, is still hampered by the small sample of well-resolved coastal sites (Carr et al. 2016).

With these limitations in mind, is it possible to link the behavioral complexity evident in the coastal contexts discussed here to these areas having acted as refugia (e.g., Marean 2011) and/or corridors for dispersal, both of which potentially encouraged cultural interconnectedness? In their paper, Carr et al. highlight previous studies on coasts as refugia both within and outside Africa, emphasizing the importance of marine resources as a reliable food source when inland settings were less favorable. Discussing climate-induced changes to the South African coastline, they suggest that population isolation may have occurred where regional geological structures prevented connections between the South African interior and its continental margins. Sealy assesses the validity of using evidence from Holocene Later Stone Age (LSA) sites (Wilton and post-Wilton) as a comparable model for demographic processes during the time of the Howiesons Poort and Still Bay. As a consequence, she makes some important arguments about population dynamics around the southern Cape coast, focusing on population size, density, expansions, contractions and connectedness during the MSA and LSA. By outlining the limitations of current datasets (e.g., problems with sample size, sampling bias, the temporal resolution of archaeological data, and the paucity of detailed paleoclimatic records), she challenges conventional interpretations of Late Pleistocene demographic processes in the region in relation to patterns of technological and behavioral complexity.

In North Africa, Jones and colleagues suggest that the Gebel Akhdar and its littoral margins in northern Cyrenaica preserved refugia for human populations during glacial periods, when populations appear to have been largely (but not entirely) confined to areas of the North African coast. During more humid episodes, on the other hand, the area appears to have been a critical fulcrum for connections via corridors with regions further to the south (e.g., trans-Saharan) and east (e.g., Nile valley). Also relevant are arguments for coastal migrations of MSA and LSA tool-makers out of Africa, and back into it, via the Sinai Peninsula and Levant (Jones et al. 2016), and of Nubian MSA tool-makers into Arabia and possibly back into Africa via the Horn (Van Peer 2016). The nature and timing of inland connections between the Maghreb and surrounding regions are addressed by Drake and Breeze, but more emphasis needs to be placed on assessing the role of corridors along coastlines themselves, particularly during the MSA. The evidence from northwest Africa (Hublin and McPherron 2012) points to a concentration of populations in

areas of the Maghreb from MIS 6-2, but how isolated or connected was this region and where did connections take place? Are important clues located in coastal areas about which we have little archaeological and hominin fossil evidence (e.g., West Africa); in fact, how viable were other coastal habitats for supporting populations? While most coastal environments may present a richness of marine food resources, it is also important to emphasize the importance of freshwater sources (Jones et al. 2016; also Dewar and Stewart 2016) capable of supporting and sustaining populations. Freshwater location and availability must have played an important role in population size and migration corridors (e.g., Faure et al. 2002), and we need to investigate water source distribution in coastal settings together with the cultural ramifications of this (e.g., the use of ostrich eggshell or skin containers).

Apart from the over-representation of certain coastlines, whose remedy must await a major Equator-ward expansion of coastal archaeological research, there are two main challenges to reconstructing Stone Age population dynamics and paleoenvironments along Africa's shores. One is to move beyond a myopic focus on coastal cave sites and towards incorporating evidence from the wider landscape, including adjacent inland areas (e.g., Carr et al. 2016; Drake and Breeze 2016; Jones et al. 2016; Dewar and Stewart 2016; Stewart et al. 2016). With respect to the southern African record and the over-representation of evidence regarding human-environment interactions from coastal sites, Burroughs (2016) notes the contrasting evidence from the Kalahari and other deep interior zones. Though genetic and archaeological evidence indicate a sustained human presence during the Late Pleistocene, substantially less is known about occupation in these vast inland areas. In northeast Libya, Jones et al. address this problem through a landscape survey of varied landforms within coastal, upland, and desert contexts, with the aim of contrasting MSA and LSA datasets from the rich coastal cave sequence of Haua Fteah against those from these different landscape settings.

The second challenge is to assess the predicaments posed by sea level fluctuations from MIS 6-2. These include mitigating the loss of evidence produced by submergence and marine erosion, and modeling human adaptive responses to sea level change. In areas of steep offshore topography, sea level changes do not appear to have significantly affected archaeological site preservation. An example of such an area is northern Cyrenaica. However, probable submergence of other sites east and west along North Africa's continental shelf may be masking important evidence of Pleistocene coastal migrations. Similarly, Dewar and Stewart note that the coastal plain of Namaqualand may have been an attractive area for human occupation during MIS 6, yet there are currently no known sites from this period, probably because they are now submerged. Marine transgressions,

particularly during MIS 5e and the early Holocene, have also resulted in data loss via the erosion of sediments within some low altitude coastal cave sites (Carr et al. 2016; Sealy 2016). Carr et al. stress that the current submergence of the South African coastal plain (Agulhas Shelf) makes it difficult to model both landscape change in these areas and the resources available to human populations. The fact that MIS 6-2 sea level change had variable impacts depending on terrestrial geomorphology and ecology means that we need to carefully think about the consequences of this with respect to both human adaptive responses and migration patterns. Yet, they also note the employment of new geophysical surveying approaches in order to better understand submerged landscapes. We suspect that advances in underwater hunter-gatherer archaeology in other parts of the world (e.g., O'Shea et al. 2014) might be fruitfully applied to shallower stretches of Africa's continental shelf.

Deserts

Some 43% of the African continent is today classified as drylands (UNCCD, UNDP, and UNEP 2009). True desert biomes include the Sahara (Drake and Breeze 2016; Cancellieri et al. 2016; Jones et al. 2016; Van Peer 2016) and Namib Deserts. Semi-arid regions include the Kalahari (Burrough 2016; Robbins et al. 2016) and Namaqualand, a semi-arid southward extension of the Namib (Dewar and Stewart 2016). By far the most expansive arid zone of all is the Sahara, the Earth's largest tropical desert, stretching from the Atlantic Ocean to the Red Sea and bordered by semi-desert and Mediterranean biomes to the north and the grasslands of the Sahel to the south. Less-extreme conditions exist in some central Saharan mountainous regions (e.g., Ahaggar, Air and Tibesti massifs), and numerous oases interrupt the desert as does Africa's longest river, the Nile. Water supply to the Sahara varied significantly from MIS 6-2. Major fluctuations are also recorded for the Nile, the most important runoff source of which is the Ethiopian Highlands. Cycles of humidity and aridity, with corresponding contractions and expansion of the desert, had a clear impact on the distribution of freshwater, plant and animal resources throughout the Sahara. Glacial and stadial periods were generally associated with hyper-aridity and desert expansion, yet these were punctuated by Saharan pluvials (Drake and Breeze 2016; Jones et al. 2016), the environmental and human consequences of which remain poorly understood. Drake and Breeze argue that well-fed rivers would have existed in the Tibesti and Ahaggar mountains during humid episodes, feeding Saharan lakes (e.g., Lake Megachad and the Chotts Megalake) and supporting high biodiversity and varied resources.

Four chapters in this volume focus on human occupation of the Sahara from MIS 6-2. Concentrating on the Tadrart Acacus and Messak massifs in the Fezzan region of Libya, Cancellieri et al. report the results of their extensive landscape surveys, including the types and densities of lithic artifacts encountered. Similarly, Jones et al. discuss patterns of MSA and LSA human occupation at the northern limits of the Sahara desert in Cyrenaica. Other chapters take a much broader view of the Saharan record. Van Peer examines patterns of human occupation across North Africa and even into Eurasia, postulating demic connections on the basis of typo-technological similarities of regional lithic assemblages belonging in particular to the MSA. Using geoproxies and dated archaeological sites, Drake and Breeze propose episodes of enhanced humidity with paleohydrological networks across the Sahara and argue that occupations by Aterian tool-makers corresponded to humid periods. This is contra Cancellieri and colleagues who associate the Aterian with generally dry conditions, and caution against assumptions that wet equates with occupation and dry equates with abandonment.

In southern Africa, past and current climate and environments in the Kalahari are given detailed treatment by Burrough and Robbins and colleagues. Burrough remarks on the existence of extreme dry and extreme wet conditions in the Kalahari from MIS 6-2, the former marked by episodes of dune building, and the latter by variably sized lakes, some of which were massive and deep (e.g., Megalake Makgadikgadi, cf. Saharan Quaternary lakes such as lakes Megachad or Megafezzan). These lakes must have had a significant impact on human occupation, as argued by both Burrough and Robbins et al. Burrough notes a spatial correlation between extensive occurrences of Paleolithic stone tools and the rivers and lakes of the Okavango-Chobe-Zambezi system. Robbins et al. provide an account of Kalahari food resources during the MSA and LSA. Evidence of fish exploitation occurs in MSA and LSA contexts, but particularly in the latter where the archaeological record indicates intensive seasonal fishing. The chapter by Dewar and Stewart focuses on Namaqualand, describing current climatic systems that affect the region and their consequences for paleoenvironments and the composition and distribution of fauna. Against this ecological framework, they propose changes in human occupation and behavior in Namaqualand from MIS 6-2. Their chapter underscores the asynchronicity between desert responses to global climate change in northern and southern Africa. Contrasting with the Sahara, they argue that Namaqualand during glacial and stadial phases was colder but wetter than today, conditions that would have facilitated higher population densities. They highlight pulses of human occupation during MIS 4 in particular, indicated by the presence of technologies comparable to those of the Still Bay and Howiesons Poort at various sites (e.g., Apollo 11). Similarly,

periods of high water availability are documented during the Last Glacial Maximum (LGM) in MIS 2, a period that would have been hyper-arid in the Sahara.

Understanding deserts as fluctuating corridors and barriers is a key issue raised by every chapter focusing on MIS 6-2 population dynamics in this biome. The challenge lies in understanding the timing, characteristics and extent of these shifts, as well as the longevity of occupation in certain desert regions. In proposing peaks in humidity in North Africa from MIS 6-2, Drake and Breeze do specify that not all humid peaks corresponded with humid corridors across the Sahara (via a network of links between Saharan mountains, lakes and rivers, linking sub-Saharan Africa and the Maghreb in particular). Instead, they indicate that the viability of certain corridors would have been highly variable from MIS 6-2. For example, their data point to a humidity peak ~154 ka during MIS 6, broadly assumed to be a period of aridity in tropical desert regions, yet they argue that this was not sufficient to 'switch on' a corridor across the Sahara. On a smaller scale, Jones et al. propose a network of paleohydrological corridors that may have linked desert and coastal biomes of northern Cyrenaica during humid episodes, arguing that MSA occupation of desert habitats was closely tied to the distribution of water (and chert) sources and that fluctuating patterns of water availability was one of the factors underlying regional variability in MSA technologies. In contrast, Cancellieri et al. recommend looking for factors other than humidity to explain human occupation patterns, challenging the argument that 'green = life'. They suggest that humans migrated along both humid and arid corridors and were well-adapted to living in arid environments (cf. Garcea 2012).

Van Peer focuses on the North African MSA record as a whole, identifying technological similarities between some MSA sites within North Africa and beyond. He argues that different regional lithic taxonomies have disguised similarities between regional MSA records. While he does not refer to any specific corridors within Africa, he does propose phases and regions of population connection and size fluctuation. While the Sahara would have presented a large barrier to human occupation and dispersals during glacial phases in particular, its 'greening' during certain periods (e.g., MIS 5e) would have presented conduits for, but also impediments to, human dispersals. One such green barrier, he suggests, was the Nile Delta, where the presence of an interglacial forest could have prevented populations from expanding along a northern Mediterranean coastal route. Similarly, during humid episodes in the Kalahari, Robbins and colleagues argue that the great extent and depth of the Makgadikgadi Megalake may have acted as a barrier against dispersals, affecting mobility and migration patterns and isolating populations. Among other factors (e.g., small sample size), they remark that this may be one reason behind

the lack of Still Bay or Howiesons Poort technologies in this region, with the paleolake having prevented their northward spread.

One important issue for consideration concerns population densities in arid zones from MIS 6-2; when and to what extent were the African deserts depopulated during this period? We may assume that there were episodes of depopulation in the Sahara and Namib deserts in particular, but perhaps there is insufficient evidence at present to confirm this. It is suggested that the Sahara was largely depopulated from MIS 4-2 (Cremaschi et al. 1998; Blome et al. 2012). Caution is recommended before accepting such broad-scale arguments, however, as it is possible that a persistence of small populations in some areas would leave barely visible, let alone dateable archaeological traces (Farr and Jones 2014). Although there are a large number of surface MSA and LSA sites from the Sahara (Cancellieri et al. 2016; Jones et al. 2016), there are very few dated sites from Saharan contexts, even those dating to humid interglacials (Drake and Breeze 2016). The absence of dated evidence from arid contexts remains a considerable problem.

During phases of greater desiccation from MIS 6-2, can we detect refugia within Africa's deserts (e.g., Larrasoña 2012)? Cancellieri et al. argue that the Aterian assemblage at Uan Tabu in the Acacus dates to MIS 4, representative of residual populations that were adapted to mountainous and arid habitats. Assuming the accuracy of the relevant dates, their evidence suggests that this area was a refuge for populations during MIS 4. In fact, some of the mountain massifs of the Sahara – the Ahaggar, Aïr and Tibesti – today harbor relict forest and Mediterranean flora and fauna (Barham and Mitchell 2008) and experience relatively high precipitation levels (Drake and Breeze 2016). It is therefore possible that areas like these harbored human populations surviving in refugia during less favorable periods during MIS 6-2. Elsewhere in the Sahara, Jones et al. comment on the existence of Saharan pluvials from MIS 4-2; these would have provided some moisture but it is unknown if this would have been sufficient to sustain populations let alone encourage expansions of population sizes and distributions. The same could be said of other areas, such as the Kharga Oasis, with its aquifer-fed artesian springs that were active during MIS 4 and MIS 2. While Van Peer notes few sites in the Lower Nile Valley during the final MSA of MIS 4/3, population densities appear to have been high in those areas that were occupied, suggesting they acted as refugia during this period. Burroughs also discusses the existence of refugia along fluvial networks in the southern African interior, where rivers fed from the tropics would have been critical water sources in otherwise water deficient regions. If hunter-gatherers aggregated near these wetter areas during Late Pleistocene dry periods, there should be increased archaeological visibility in these areas. Although MSA and

LSA sites (often surface occurrences) are numerous in the region, this has yet to be tested archaeologically, and very few of these sites are excavated and dated. The possibility of refugia existing within otherwise extreme arid environments (e.g., along river corridors, uplands or oases) is something that should be incorporated into models of past population dynamics within African deserts, as it already has been on other continents (e.g., Veth 1989, 1993), including their role in eliciting social, technological, and demographic changes (cf. Van Peer 2016).

Critical to discerning past population dynamics in deserts is the need to understand the complex relationships between deserts and adjacent biomes, in particular the impacts of spatiotemporal fluctuations in ecotones from MIS 6-2. In a number of localities in northern and southern Africa, for example, desert and coastal biomes are often directly adjacent or situated nearby. Some chapters have modeled population movements between coastal settings and their variably arid hinterlands (Dewar and Stewart 2016; Jones et al. 2016; Stewart et al. 2016). It is the interfaces between these different biomes that may have provided ecotonal advantages for hunter-gatherer groups, resulting in adaptive responses to variable resource types and distributions, with possible technological consequences. Jones et al. suggest that such adaptive responses to shifting habitats are reflected in the MSA and LSA records of Cyrenaica. Similarly, there are relationships between deserts and woodlands/rainforests (see below). Tropical rainfall over equatorial Africa feeds many rivers that terminate in or run through deserts. These include the Niger, Nile and Chari in North Africa, and, in southern Africa, the Okavango, which terminates as a delta in the northwest Kalahari. River systems probably acted as refugia zones or corridors at times from MIS 6-2 (e.g., Basell 2008; Stewart et al. 2016), and most notably during MIS 5e with the paleoriver and paleolake systems of the Sahara (e.g., Drake and Breeze 2016). In the Kalahari, Burrough argues that transitional periods during MIS 6-2 were marked by large-scale landscape and ecological changes, necessitating adaptive responses in the form of innovation and/or mobility. Transitional periods could have brought benefits as new ecotones were established. Understanding the implications of the shifts between biome boundaries adds an additional level of complexity, yet these shifts could be a driving force behind variable adaptive responses and evolutionary trajectories within and beyond such geographic regions.

In attempts to understand past population dynamics within and across desert biomes from MIS 6-2, we encounter three main challenges: managing the considerable variability within African desert environments; coping with preservational problems; and identifying drivers of hydrological change. Deserts are extraordinarily heterogeneous environments, and understanding past human adaptations to the great spatial and temporal variability within deserts, let alone

their ecotonal habitats with adjacent biomes, constitutes a significant challenge. Dunefields, mountain massifs, coastlines, river systems, oases, and paleolakes within deserts presented hunter-gatherer populations with very varied opportunities and constraints. Although aridity is frequently emphasized as a driver of cultural change and innovation (e.g., Clark 1960), arguments for climatic *variability* as more influential are gaining traction (Burrough 2016; Jones et al. 2016; Stewart et al. 2016). For example, Burrough (2016) states that “In the context of past population dynamics, overarching climatic theories remain largely irrelevant, since it is regional environmental (rather than climatic) variability to which hominins are likely to have responded,” where the spatial complexities of landscape and regional climate dynamics should be taken into greater account. For the Sahara, Cancellieri et al. make two important points of relevance. First, they emphasize that in central Saharan contexts, minor variations in rainfall can alter delicate equilibriums. Second, they emphasize that the Sahara possesses a considerable variety of ecological niches that can support human populations today. This suggests that viable habitats for hunter-gatherers can open and close within this vast desert with variable frequency, nuances that should be factored into demographic models.

In order to reveal how variability impacted past population dynamics, high-resolution dated paleoenvironmental records are essential, together with *in situ* archaeological contexts. This brings us to the second challenge – the problem of preservational issues in desert environments. Burrough remarks that the spatially diverse and fragmentary nature of geoproxy records has resulted in climate change models that are often contradictory and oversimplified. Similarly, it may not be possible to identify a Saharan corridor that corresponds to the MIS 6 humidity peak proposed by Drake and Breeze, simply due to an absence of preserved sediments and hence paleohydrological data. This, together with a lack of dated contexts from the Sahara, makes it very difficult to correlate human responses with climate change. Archaeological evidence in desert environments is most often encountered on the desert surface in erosive and deflated contexts, often as palimpsests (Cancellieri et al. 2016; Jones et al. 2016; Burrough 2016; Robbins et al. 2016; Dewar and Stewart 2016). Conversely, much cultural material is also inaccessible beneath deep sediment accumulations. Dating MIS 6-2 archaeological evidence in desert environments is thus highly problematic and often relies on subjective techno-typological correlations. This is a problem that recurs in each desert chapter. Although few in number, there are some notable excavated sites in desert contexts that have provided significant data; for example, Uan Tabu and Uan Afuda (Cancellieri et al. 2016), White Paintings Rockshelter (Robbins et al. 2016), Apollo 11 and Spitzkloof (Dewar and Stewart 2016). Furthermore, one benefit of desert archaeology

is the high visibility of artifacts, albeit in surface contexts, meaning that broad landscape-scale patterns of artifact types, technologies, and densities are achievable that would otherwise be very difficult in other environments (e.g., woodlands, rainforests, or densely populated areas today).

The final challenge is to determine the drivers of hydrological changes within deserts. Again, understanding local variability in terms of landscape and regional climate dynamics is critical here. For example, do river and lake activations within desert biomes represent local amelioration or changes occurring in more proximal parts of hydrological systems, such as equatorial zones (e.g., Burroughs)? Drake and Breeze comment that there is currently a poor understanding of the interplay between the African monsoon and the North Atlantic and Mediterranean westerlies with respect to the extent of Saharan ‘greening’. Perhaps instead, enhanced humidity simply resulted in the reactivation of rivers that flowed through otherwise arid zones. In Namaqualand, Dewar and Stewart propose that colonization of the coastal plain by grasslands during marine regressions (during early MIS 2 in particular) was a consequence of two alternate mechanisms: increased precipitation with westward movement of the coastline, or reduced evaporation as a result of lower temperatures. These examples highlight that there were probably multiple potential drivers of paleohydrological change affecting African desert environments. These may have been proximal and/or distal, with specific regional landscape-driven and climate-driven idiosyncrasies that contributed to a complex yet delicate balance between wet and dry.

Grasslands, Woodlands, and Rainforests

Between $\sim 20^\circ$ S and $\sim 20^\circ$ N, Africa’s drylands give way to the grasslands, woodlands, dry forests, and rainforests that dominate its core. Together, these biomes constitute well over half of the continent. The terms grassland and woodland as applied to modern African environments are nebulous and often subsume a spectrum of vegetation types, including shrubland, parkland, thicket, grassland savanna, woodland savanna, and dry forest. Africa’s grasslands are predominantly savannas – that is, seasonally dry, edaphic tropical/subtropical grass-dominated plant communities with discontinuous tree cover (Osborne 2000; Timberlake et al. 2010). Savanna is the continent’s largest single biome and Africa’s are the world’s most extensive (Osborne 2000). In contrast, temperate grasslands are much more restricted, found only in southern Africa’s Highveld and Maloti-Drakensberg Mountains (Mucina and Rutherford 2006; Stewart et al. 2016) and highland Ethiopia. Unlike true savannas, these vegetation zones experience frost (Lewis

and Berry 1988). Africa south of the rainforests is dominated by the enormous Miombo and Mopane humid savanna woodlands, which cover most of Angola, southern Democratic Republic of Congo (DRC), Zambia, southern Tanzania, Zimbabwe, Malawi and Mozambique. South of this are the dry savanna parklands of eastern Namibia, Botswana and northern South Africa that in places grade into semi-desert and desert. Moving north of the rainforests, three increasingly dry savanna belts (the Guinea, the Sudan and the Sahel) span nearly the continent’s full width from Senegal to Sudan.

Where the southern and northern grasslands meet, to the east of the rainforests, are the savannas of East Africa, most famously exemplified by the Serengeti with its extraordinary mammalian, bird, and insect diversity and biomass. Two chapters deal with East Africa from MIS 6-2 (Faith et al. 2016; Lahr and Foley 2016). Both draw attention to the region’s mosaic-like ecological structure underpinned by its complex climatic and geological history. Lahr and Foley synthesize a wide range of archaeological, fossil, and genetic evidence to explore patterning within East Africa and draw inter-regional comparisons. They suggest that the high habitat heterogeneity of East Africa would have promoted relative population stability through MIS 6-2 by providing a ‘refugial network’, or “set of independent, potentially asynchronous *refugia* linked by semi-contiguous geographic corridors” (Lahr 2013). By facilitating dispersals between relatively reliable and closely situated resource patches, such a network could have increased the options available to human groups adjusting to rapid climate changes or phases of reduced resource availability. A similar argument has been advanced by Basell (2008), who identifies the region’s lake margins, rivers, and highlands as good candidates for Pleistocene human refugia, particularly through the prolonged aridity of MIS 6.

Regional linkages are also integral to Faith et al.’s chapter, which explores the affects of East Africa’s environmental history on human paleodemography using insights from ungulate biogeography. Drawing on new paleontological data from Rusinga and Mfangano Islands in Lake Victoria, they argue that fluctuations in moisture availability, atmospheric CO₂, and topographic changes through the Middle and Late Pleistocene prompted major shifts in ungulate ranges. The presence in these bone assemblages of a diverse mix of ungulate taxa that today occupy discrete, often distant habitats indicates their deposition occurred during drier phases when Lake Victoria and others shrank and/or disappeared and grasslands expanded, interlinking the region via biogeographical corridors. That such corridors were also important for humans is something they suggest is reflected in the region’s distribution of MSA lithic technologies. Small MSA bifacial points on the islands bear similarities to assemblages in the Rift Valley, which

may signal movement from or interactions with regions further east during glacial or stadial phases. These point assemblages are consistently associated with proxy evidence for grassy environments. They contrast with woodland-associated assemblages of Lupemban affinity at other sites that hint at connections in the opposite direction (to the west) during warmer/wetter phases when Africa's forested core expanded.

Faith and colleagues thus emphasize glacial and stadial phases as promoting increased intra-regional connectivity. Interestingly, this is contrary to Basell (2008: 2496), who suggests that during these periods humans contracted into refugia that were "largely disconnected, separated by areas of open grassland, semi desert and desert" and "acted as barriers between hominin populations." Under more humid conditions, Basell (2008) argues that the distribution of human populations broadened with forest expansions, noting a tight correspondence in East Africa between MSA sites and woody settings. Conversely, Faith et al. (2016: 235) suggest that "during interglacials, the expansion of tropical forests across equatorial East Africa created a barrier that fragmented populations and restricted gene flow." Such interpretive differences underscore the desperate need throughout Africa for continuous, high-resolution regional paleoenvironmental archives that can provide data on *resource availability*, rather than just a broad sense of the predominant vegetation. Ideally, such archives should then be evaluated against regional archaeological records to identify the resource structures in which material cultures – and by extension people and/or information – either coalesce or fragment (cf. Mackay et al. 2014). Neither dry savannas nor dry forests typically impede foragers in the 'ethnographic present', and while rainforests and true deserts can (but by no means always do) act as barriers, the challenge is to understand whether, when, and the extent to which they may have done so in the past.

This is particularly pressing in East Africa, where habitat variability through time and space may have provided the selective context in which our species evolved. The location and timing of modern human origins within Africa are dealt with substantively by Lahr and Foley in their chapter. Dismissing recent molecular evidence favoring a southern African center of origin (Henn et al. 2011), they advocate East Africa as the most likely backdrop to both our biological and behavioral evolution. For support they cite the region's potential for harboring refugia (or 'refugial networks'), its uniquely ancient modern human fossil evidence (e.g., Omo Kibish, ~195 ka, McDougall et al. 2005; Herto, ~165 ka, White et al. 2003) and its early MSA archaeological record (e.g., Gademotta, >276 ka, Morgan and Renne 2008; Sahle et al. 2013). The timeframe they favor is gradual, with our phenotypic roots stretching into MIS 9-7 even if the first *sapiens*-specific morphological

traits only appear in earliest MIS 6, and the largest strides toward cognitive complexity occurring ~300 ka with the advent of prepared core technologies (Foley and Lahr 1997). While their argument merits serious consideration, they air a debate that is beyond the scope of this introduction. Here we wish only to point out that the findings of Faith et al. suggest the region's patchwork ecology may be a largely interglacial phenomenon, with colder and drier glacial stages producing more homogeneous habitats with greatly diminished surface water. If so, this has implications for the extent to which the current ecological structure of East Africa can be used to support models of where *Homo sapiens* survived or speciated through a putative population bottleneck (Lahr and Foley 1998; Garrigan and Hammer 2006; Fagundes 2007; but see Sjödin et al. 2012), and re-emphasizes the need for crisper paleoenvironmental resolution at the local scale.

There is one landscape feature that would have always ensured African hunter-gatherers a degree of habitat heterogeneity, namely mountains. Widely spaced along the periphery of the continent's immense interior plateau, Africa's mountain systems are essentially biogeographical islands of cold-adapted, species-rich habitats punctuating the warmer, more homogeneous lowland 'sea'. Their broad geographic distribution, spanning the continent's full ~70° of latitude, with numerous geological substrates and multiple rainfall zones, makes them extremely diverse. Nevertheless, all the major mountain zones are stratified by distinct, altitudinally mediated vegetation belts, with numbers ranging from 3-4 in the Atlas and Maloti-Drakensberg and up to 6-8 in highland Ethiopia, the Rwenzori, Mount Kenya, and Kilimanjaro. While the highest afroalpine zones probably always discouraged prolonged or even sporadic human activity, mid-altitude afromontane belts would have offered foragers dividends for relatively minor increases in elevation. Broadly, these include greater resource diversity per unit area of terrain and reliable supplies of key resources, notably fuelwoods, plantfoods and medicines, seasonal hunting opportunities, rockshelters, high-quality volcanic or sedimentary toolstones and, perhaps most critically, fresh-water. The latter – supplied by orographic rainfall and afroalpine snowmelt – may have been especially vital when seasonal or longer term changes in precipitation and/or evapotranspiration resulted in dwindling aquifers further downslope. In tropical Africa, highland settlement may also be expected to correlate with phases of marked humidity, conditions that encourage the spread of vector-borne parasitic diseases like trypanosomiasis and malaria that are absent or rare ≥1500 m a.s.l. (Ford 1971; Lindsay and Martens 1998).

Having long taken a backseat to other biomes, research into early human engagements with afromontane environments seems to be accelerating. Recent excavations by Stewart and colleagues in the Maloti-Drakensberg

Mountains of southern Africa are a case in point (Stewart et al. 2012, 2016). Their chapter presents the results of a multiproxy paleoenvironmental analysis of the ~85 kyr sequence at Melikane Rockshelter in the temperate grasslands of highland Lesotho (1800 m a.s.l.). Humans visiting the site through MIS 5-2 consistently encountered a landscape dominated by alpine grasses that today grow at higher altitude, suggesting a prevalence of cool conditions with subtle changes in temperature and moisture. The recurring presence of woody riparian taxa suggests precipitation was consistent enough to support water-loving vegetation along the deeply incised watercourses. Relating Melikane's record to others in the wider region, Stewart et al. posit a dual-source model of highland population influx. Regional warming, they suggest, would have encouraged mountain incursions from the adjacent coastal forelands because of either population increase there (push) or ameliorated conditions at altitude (pull). Phases of regional aridity or instability, however, more likely provoked influx originating in the Karoo Desert to the west, from which groups could follow the Orange-Senqu River to its stable headwater sources in the highlands. The latter appear to have been especially attractive during one such phase ~46–38 ka, when Melikane registers its most sustained occupation (Stewart et al. 2012). In contrast, intense cold – such as that experienced during the LGM and parts of MIS 4 – appears to have deterred highland incursions regardless of other environmental variables.

Recent work by Mercader and colleagues (2013) further north on Mozambique's Niassa Rift flank reveals a similar pattern. There, phases of intensified afromontane activity through MIS 5-3 occurred when paleoecological evidence suggests water availability was high in the highlands and low in the lowlands, echoing the situation in the Maloti-Drakensberg. Unlike Lesotho's temperate grasslands, Niassa's highlands show evidence of being densely forested at such times, prompting Mercader et al. (2013: 328) to wonder whether a 'montane woodland archipelago' linking southern and East Africa might have facilitated human dispersals across (and perhaps out of) the continent. Such a scenario corresponds well with Basell's (2008) findings and is tentatively consistent with recent work at Mochena Borago Rockshelter in highland Ethiopia (Brandt et al. 2012: 51). Nevertheless, all of these studies demonstrate the rewards of investigating human and environmental signatures in afromontane zones. These sites provide important counterparts to the better-known lowland hotbeds of research by filling hitherto unexplained 'gaps' in those records while enhancing our understanding of the range of selective pressures under which our species' behavioral repertoire evolved (Stewart et al. 2012; Dewar and Stewart 2012).

Returning to lower altitudes, Africa's largest lowland zone is dominated by the least understood biome of all: the

rainforests. Africa's rainforests are better defined both ecologically and geographically than its grasslands and woodlands. These are the closed-canopy, stratified forests in equatorial areas humid enough for year-round growth. Annual precipitation averages 1600–2000 mm, annual humidity >80%, and the short dry season experienced in most areas is not severe enough to prevent plant growth as in grasslands and dry woodlands. Nevertheless, Africa's rainforests are significantly drier than those on other continents (Bonnefille 2011). Average monthly temperatures are high (≥ 17 °C) though not extreme, and diurnal and yearly temperature fluctuations are very low. Since nutrients in rainforests are locked up in plant biomass and recycle rapidly rather than enriching the soil, these ecosystems are more sensitive to climatic and anthropogenic changes than woodlands and grasslands (Lewis and Berry 1988). Africa's main rainforest zones center on the Congo Basin and West Africa's south coast. High levels of surplus runoff in the former generates Africa's largest river in terms of discharge (and second longest after the Nile). Yet neither the Congo, the Niger, nor any but the smallest central/West African rivers flow entirely within the present-day rainforest, passing instead through or into drier, more open woodland/grassland biomes (Lewis and Berry 1988; Burrough 2016). The Niger, for example, originates in well-watered highlands on the westernmost rainforest fringe, then flows northeast through the increasingly arid Sudanian and Sahelian belts to the southern Sahara, before returning to the rainforest to discharge at the Gulf of Guinea. Such rivers may have provided conduits for human movement and communication through MIS 6-2, both within the equatorial core and between it and adjacent biomes.

Our decision to group Africa's rainforests, woodlands, and grasslands into a single section of this book stems largely from the uneven geographic distribution of chapter topics. There are, however, also ecological grounds for considering them together as the distribution of these biomes was in flux from MIS 6-2 due to fluctuations in moisture balance. During drier climatic episodes a range of evidence suggests the rainforests fragmented into isolated refugia interspersed with open-canopy woodlands and grass savannas, with periods of enhanced moisture promoting widespread forest re-expansion (e.g., Van Noten 1982; Brook et al. 1990; Maley 1996; Jahns et al. 1998; Dupont et al. 2000; Runge 2000, 2001a, b; Bonnefille 2011). During the LGM, for example, it is estimated the African rainforests were ~15–30% of their current size, as compared to ~50% for those of the Amazon Basin (Anhuf 2000; Anhuf et al. 2006). The contrast between continents is due to tropical Africa's lower rainfall relative to other equatorial areas, which appears to have made the ecological consequences of Pleistocene climatic changes more extreme (Anhuf et al. 2006; Bonnefille 2011). Without question, such broad-brush

scenarios oversimplify far more complex regional environmental histories (Mercader et al. 2000; Cornelissen 2002, 2016). The LGM refugia, for example, seem more likely to have been numerous, widely dispersed riverine and montane patches rather than large, relatively homogenous remnant rainforest cores as was previously thought (Moore 1998; Cornelissen 2002, 2013). Even today, Africa's rainforests are far from uniform, with variations in seasonality and topography both significantly influencing vegetation distributions (Bonfille 2011). However, terrestrial paleoenvironmental archives in this huge region remain scarce, with fewer still reaching back before MIS 2 (e.g., Scholtz et al. 2011; Shanahan et al. 2012). Marine cores off West Africa are longer and more continuous (Dupont et al. 2000) but lack spatial precision, and complex transport processes of pollens and spores can impede even vegetation reconstructions of terrestrial source areas that are closely adjacent. Confounding matters further is the strong likelihood that today's rainforest 'remnants' represent inapposite analogues for those of the past due to long-term human modification (Mercader 2003: 2).

These and other issues hamper detailed reconstructions of the environments in which lowland tropical Africa was first peopled and subsequently inhabited. The subsistence challenges that confront hunter-gatherers occupying dense tropical forests are well known. Carbohydrate resources in rainforests are typically rare, inaccessible, and/or toxic, while prey taxa tend to be small, dispersed and often nocturnal. The extent to which such resource structures might have deterred prehistoric foragers from populating the world's rainforests has been widely debated (Headland 1987; Bailey et al. 1989; Townsend 1990; Bailey and Headland 1991; Colinvaux and Bush 1991; Endicott and Bellwood 1991; Mercader 2002, 2003; Barton 2005). The most extreme view holds that these environments were uninhabitable until the advent of farming when rainforest productivity increased through deforestation and exchange with agriculturalists ensured sufficient carbohydrates (Bailey et al. 1989). Africa has played a central role in contesting such views, with research conducted at various central African sites over the past two decades demonstrating that the human capacity to cope with dense closed-canopy forests pre-dates agriculture by a substantial margin of at least 20 kyr (Mercader et al. 2000; Mercader 2002, 2003). Emphasis has therefore shifted from the question of whether pre-agricultural foragers were able to inhabit Africa's rainforests towards fuller considerations of Pleistocene adaptations across the region. As with paleoenvironmental reconstruction, massive gaps in knowledge – in this case caused or exacerbated by severe taphonomic vagaries, logistical difficulties and political instability – make the task herculean.

In the final two chapters of this section, Cornelissen and Taylor take up the challenge. Both authors offer cogent syntheses of what is currently known about the Stone Age

occupation of central Africa, drawing on a breadth of sources to maximize the data available. Cornelissen focuses on the rainforest's eastern zones in the northeastern DRC, an area that includes the Ituri forest. Until recently, little was known of this region's deep prehistory despite it being home to some of the world's best-studied hunter-gatherer groups (e.g., Turnbull 1961; Cavalli-Sforza 1986). Compiling data from published reports and unpublished museum collections, Cornelissen investigates the spatial distribution of virtually every recorded Stone Age occurrence in the region. As documented elsewhere in the central African rainforests, her research area's lithic assemblages are dominated by two very distinct traditions: (1) those lacking bifaces and typified by highly informal quartz microliths; and (2) others with bifaces, which can include foliates with clear Lupemban affiliation. These sharp technological contrasts reflect major temporal differences, as the two industries effectively bookend MIS 6-2.

At the few dated rockshelters where they occur, quartz microlithic assemblages span late MIS 3 to the late Holocene and have been described as LSA. Though more restricted in space than bifacial assemblages (Cornelissen 2016), their association with a range of paleoenvironmental proxies from forested to open suggests a versatile, expedient adaptation whose ~40 kyr duration testifies to its success (Cornelissen 2002). As Cornelissen points out, however, such diverse ecological associations and temporal continuity limits this technology's utility for demographic reconstruction. Moreover, it seems increasingly unlikely that successful rainforest colonization depended on innovations in lithic technology (Mercader 2003). At Ishango 11 in the Semliki Valley of the easternmost DRC, quartz microlithic tools have been recovered from LGM contexts alongside finely crafted bone harpoons and fish remains. The bone technology and species composition at Ishango 11 are nearly identical to those at the nearby site of Katanda with dates nearly four times as old (~80 ka; Feathers and Migliorini 2001). That fluvial fauna were being effectively captured in equatorial Africa by late MIS 5 may hint at the timing of permanent human settlement in the region, since such resources "may be important for exploring and exploiting an environment such as the rainforest with swamps and an abundant network of waterways" (Cornelissen 2016). But given the limited bone preservation in dense tropical forests, Cornelissen suggests the role of aquatic resources in early adaptations to such environments might be better explored via genetics.

Cornelissen's other main assemblage type – those with bifacial tools – appear to represent "a more ancient and more widely spread hunter-gatherer habitation of the region" (Cornelissen 2016). Though known from MIS 2 and Holocene contexts in west-central Africa (Cornelissen 2002), bifacial forms in the eastern forests are clearly older. Assemblages include handaxes, core-axes and picks, but the most intriguing are those classed as Lupemban, which can

include blades and backed blades, prepared core and leaf-shaped points, and – most conspicuously – elongated, invasively flaked lanceolates that constitute the industry's *fossiles directeurs*. Discussion of the Lupemban brings us back to J.D. Clark's pioneering thoughts on population dynamics in Stone Age Africa. Clark envisaged the Lupemban as an adaptation to central Africa's dense forests whose innovation catalyzed the region's human colonization. This hypothesis, conceived over a half-century ago, remains untested. Yet recently obtained late Middle Pleistocene dates for Lupemban assemblages from key sites that include pigments and backed artifacts (Barham 2000, 2001, 2002a, b, 2012), taken together with the general African reorientation of behavioral origins research (McBrearty and Brooks 2000; Henshilwood and Marean 2003), render it today more tantalizing than ever.

In a chapter dealing exclusively with the Lupemban, Taylor provides a comprehensive and much-needed reappraisal of this enigmatic technocultural phenomenon. He generates a database of every reported Lupemban (or related) occurrence, which is then systematically interrogated to assess the data's robusticity by culling problematic cases. The process reveals the staggering extent of our ignorance; adequate paleoenvironmental proxy evidence, for example, exists for only 5% of Lupemban sites, a mere 17% have chronometric dates, and only 3% are dated using radiometric techniques capable of reaching beyond radiocarbon. Many occurrences lack the requisite documentation to establish provenance or affirm Lupemban affiliation, others are surface finds, and all have suffered some form of disturbance. In fact, at only two sites have Lupemban artifacts been recovered from coherent stratigraphic sequences – Twin Rivers and Kalambo Falls – both situated in Zambia's savanna woodlands. As Taylor notes, such extreme impoverishment “precludes the derivation of precise data pertaining to [the Lupemban's] techno-typological composition and spatiotemporal variability, and hampers attempts to test its potential behavioral significance” (Taylor 2016: 289). Nevertheless, the site distributions Taylor generates from his database – which serve as an independent, updated counterpoint to those in Clark (1967) – lend weight to Clark's original correlation of the Lupemban with wooded habitats and challenge arguments for its strict association with expanded glacial-phase grasslands (e.g., Banks et al. 2006). If a woodland correlation can be taken to indicate an emergence during the MIS 7 interglacial (~240–190 ka) (Barham 2001, 2012), the Lupemban clearly merits serious consideration as an archaeological residue of the first rainforest foragers and thus an early signature of behavioral complexity not unlike modern hunter-gatherers.

The Lupemban's seemingly long duration and continuity with the subsequent Tshitolian hints at high overall population stability in central Africa from MIS 6-2. Like the

quartz microlithic industries that succeed it, viewing the Lupemban not as a biome-specific adaptation but rather as a flexible solution to foraging in shifting, variably wooded environments may help explain this longevity. Taylor points out that such a diverse, sophisticated technological repertoire probably performed well in both open and closed environments, a view supported by the limited proxy data available (van Zinderen Bakker 1969; Bishop and Reynolds 2000; Taylor et al. 2001). As with certain coastal and afromontane areas, intermediately wooded parts of central Africa probably acted as human refugia at times, though the locations of optimal areas would have changed as humid rainforests and dry grasslands waxed and waned with glacial cycles. As a corollary, high population stability also makes it plausible that the region contributed source populations to human dispersals both within and beyond Africa. Even if foragers only developed the adaptive tools necessary to thrive in the densest rainforests from MIS 3, the region may have always been more attractive when the canopies had thinned. As discussed by Cornelissen (2002), it is likely that the ecological reconfigurations and ecotones so created would have profoundly impacted the distributions of human groups through Africa's equatorial core from MIS 6-2 and perhaps before (see debate in Herries 2011; Barham 2012). For the moment, though, the Lupemban's spatiotemporal resolution is far too coarse to properly assess Clark's hypothesis, let alone assess the industry's broader evolutionary significance. The timing and ecological context of the earliest human incursions into central Africa will remain obscure until better chronostratigraphic sequences are discovered and developed. Likewise, suggestions that the Lupemban holds some sort of ancestral relationship to later, better-known bifacial MSA industries in North (the Aterian) and/or southern Africa (the Still Bay) must, in the absence of an improved central African record, remain speculative (Henshilwood 2008; Van Peer 2016).

Conclusion

This volume represents a first concerted effort to assess Stone Age population dynamics throughout Africa, and how these changed with fluctuations in global climate and more localized environments. The choice of MIS 6-2 is driven by multidisciplinary evidence that the last ~200 kyr of the Pleistocene saw the consolidation of longer term trends toward the evolution of hominins physically and cognitively identical to ourselves. This was also the time interval during which modern human groups undertook multiple dispersals from the continent along various routes, culminating by late MIS 2 in the colonization of every habitable corner of the globe. Thus while earlier stages of the Middle Pleistocene

were clearly fundamental in setting the stage for modern human evolution, the pronounced climatic and ecological volatility of MIS 6-2 hosted the final act. There are strong indications across multiple records that the distribution of human populations across Africa from MIS 6-2 was highly discontinuous. This is registered in the archaeological record by regional artifact traditions that alternately coalesce, fragment, or disappear entirely, and corroborated in the human fossil and genetic records by a high degree of morphological variability (Grine 2016) and evidence for deep time population structure (Soares et al. 2016), respectively.

However, to make real progress towards reconstructing population dynamics and understanding their evolutionary implications in Africa and beyond, we must build stronger bridges between archaeology, paleoenvironmental science, human paleontology and genetics (e.g., Lombard et al. 2013). We must work harder at disciplinary interfaces to integrate datasets that have inherently different resolutions and speeds of progression. How, for example, can we better assimilate insights from population genetics, which accrue at breakneck speeds but at relatively coarse historical resolution, into regional archaeological records, which are sharper but whose construction is painstakingly slow? Reconciling datasets *within* disciplines is also a major challenge, particularly when they represent different scales of phenomena. For example, the global-scale climate changes seen in the marine or ice core records must be interpreted in relation to their impact on regional- or local-scale paleoenvironments as reconstructed from discontinuous terrestrial archives. Similar challenges arise when attempting to compare chronologies derived from diverse dating techniques with different error margins, or interpreting variability in artifact form and frequency from a single site in relation to the full geographic and temporal span of that industry.

To examine population dynamics and their relationship to paleoenvironments is to examine change, and understanding the meaning of changes we detect is paramount. Disentangling demographic changes (e.g., population replacement) from the assimilation of external ideas (e.g., through diffusion) or *in situ* processes (e.g., cultural adaptation to environmental shifts) lay at the very core of inquiry into this topic. With such a shortage of human fossils throughout Africa from MIS 6-2, this will necessarily depend on more refined technological analyses of lithic industries and other material culture indicators. Similarly, translating coarse paleoenvironmental inferences into more explicit statements about resource abundance and structure is essential for establishing the human-scale ecological contexts needed for assessing adaptive change. On the other hand, reconciling our understanding of archaeological industries of seemingly extraordinary duration, including the Lupemban and Aterian, with those recently shown to be extremely short-lived, such as the Still Bay and Howiesons Poort, underscores the challenges of

explaining continuity, and particularly of decoupling gross typological similarities across space and time from finer-scale shifts in technology that may prove more informative.

The ultimate goal towards which this book is merely a first step is to produce a diachronic, continental-scale understanding of human biogeography for Stone Age Africa. Similar efforts undertaken on other continents, particularly Australia, have proven highly fruitful (e.g., Veth 1989, 1993, 2005; O'Connor et al. 1993; Smith 1993, 2013; Hiscock and Wallis 2005; Hiscock 2008; Smith et al. 2008; Williams 2013). Perhaps our greatest hindrance in Africa is the extreme geographical unevenness and thus overall paucity of data. Though our knowledge of Stone Age Africa has grown immensely in the five decades since J.D. Clark (1960) crafted his wish list, vast tracts of the continent remain Paleolithic question marks. Poor coverage is particularly acute in West and central Africa, but also in substantial areas of the continent's north, east and south. While the chapters in this volume inevitably reflect this bias, they also sample the exciting array of datasets, approaches and ideas that are being brought to bear on understanding population dynamics in ancient Africa, their paleoenvironmental correlates and their evolutionary significance. Mapping and dating shifts in human biogeographical phenomena, including corridors, barriers, refugia, and abandonment zones, and how these articulate with regional archaeological, fossil and genetic records, should help unlock the secrets behind our species' biological and behavioral florescence.

Acknowledgments We thank Graeme Barker and Peter Mitchell for their thoughtful comments on an earlier draft of this introductory chapter.

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