



Microhabitat Variability in Human Evolution

Robert Patalano^{1*}, Rebecca Hamilton^{1,2,3}, Emma Finestone¹, Noel Amano¹,
Phoebe Heddell-Stevens¹, Makarius Itambu^{1,4}, Michael Petraglia^{1,5,6,7} and
Patrick Roberts^{1,5,8*}

¹Max Planck Institute for the Science of Human History, Jena, Germany, ²College of Asia and the Pacific, Australian National University, Canberra, ACT, Australia, ³Australian Research Council Centre of Excellence for Australian Biodiversity and Heritage, The Australian National University, Canberra, ACT, Australia, ⁴Department of Archaeology and Heritage Studies, University of Dar es Salaam, Dar es Salaam, Tanzania, ⁵School of Social Science, The University of Queensland, Brisbane, QLD, Australia, ⁶Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, DC, United States, ⁷Australian Research Centre for Human Evolution (ARCHE), Griffith University, Brisbane, QLD, Australia, ⁸Archaeological Studies Program, University of Philippines, Quenzon City, Philippines

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*Correspondence:

Robert Patalano
patalano@shh.mpg.de
Patrick Roberts
roberts@shh.mpg.de

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Climate variability and hominin evolution are inextricably linked. Yet, hypotheses examining the impact of large-scale climate shifts on hominin landscape ecology are often constrained by proxy data coming from off-site lake and ocean cores and temporal offsets between paleoenvironmental and archaeological records. Additionally, landscape response data (most commonly, records of vegetation change), are often used as a climate proxy. This is problematic as it assumes that vegetation change signifies global or regional climate shifts without accounting for the known non-linear behavior of ecological systems and the often-significant spatial heterogeneity in habitat structure and response. The exploitation of diverse, rapidly changing habitats by *Homo* by at least two million years ago highlights that the ability to adapt to landscapes in flux had emerged by the time of our genus' African origin. To understand ecosystem response to climate variability, and hominin adaptations to environmental complexity and ecological diversity, we need cross-disciplinary datasets in direct association with stratified archaeological and fossil assemblages at a variety of temporal and spatial scales. In this article, we propose a microhabitat variability framework for understanding *Homo*'s adaptability to fluctuating climates, environments, and resource bases. We argue that the exploitation of microhabitats, or unique ecologically and geographically defined areas within larger habitats and ecoregions, was a key skill that allowed *Homo* to adapt to multiple climate zones and ecoregions within and beyond Africa throughout the Pleistocene.

Keywords: microhabitat variability, human evolution, climate change, paleoecology, africa

INTRODUCTION

Climatic and environmental variability are often presented as major influencers on human evolution (Vrba, 1995b; Potts, 1998a; Trauth et al., 2010; Cerling et al., 2011; deMenocal, 2011), including the origins and diversification of *Homo* or the development of specific stone tool technologies (Potts et al., 2020; Lupien et al., 2021; Schaebitz et al., 2021). Variable Pliocene-Pleistocene climate for example, may have required hominins to effectively respond to the extreme selection pressures imposed by dynamic climatic systems, leading to genetic and morphological change and technological innovation (e.g., Committee on the Earth System Context for Hominin Evolution,

2010). It is even argued that changes in African climate and hominin extinction, speciation, and behavioral events were inextricably linked over the past 6 million years (deMenocal, 2011). The last appearance of *Australopithecus afarensis* around 2.9 Ma (Campisano and Feibel, 2008; Alemseged et al., 2020), the appearance of the genus *Homo* at 2.8 Ma (Villmoare et al., 2015), the emergence of *Paranthropus* after 2.7 Ma (Coppens, 1968; Harrison, 2002), and the earliest evidence for Oldowan stone tools at 2.6 Ma (Semaw et al., 1997; Braun et al., 2019) appear to overlap with Northern Hemisphere glacial intensification, faunal changes, aridification, and grassland expansion in Africa (Bobe and Eck, 2001; Semaw, 2003; Evolution, 2010; deMenocal, 2011). Moreover, the emergence of *Homo erectus* and subsequent migrations out of Africa seemingly occurred when subtropical temperatures cooled around 1.9 Ma (Ravelo et al., 2004), while the appearance of the Acheulean at ~1.75 Ma has been suggested to coincide with increases in African wind-borne dust and aridification near 1.8 Ma (deMenocal, 2004; Lupien et al., 2018).

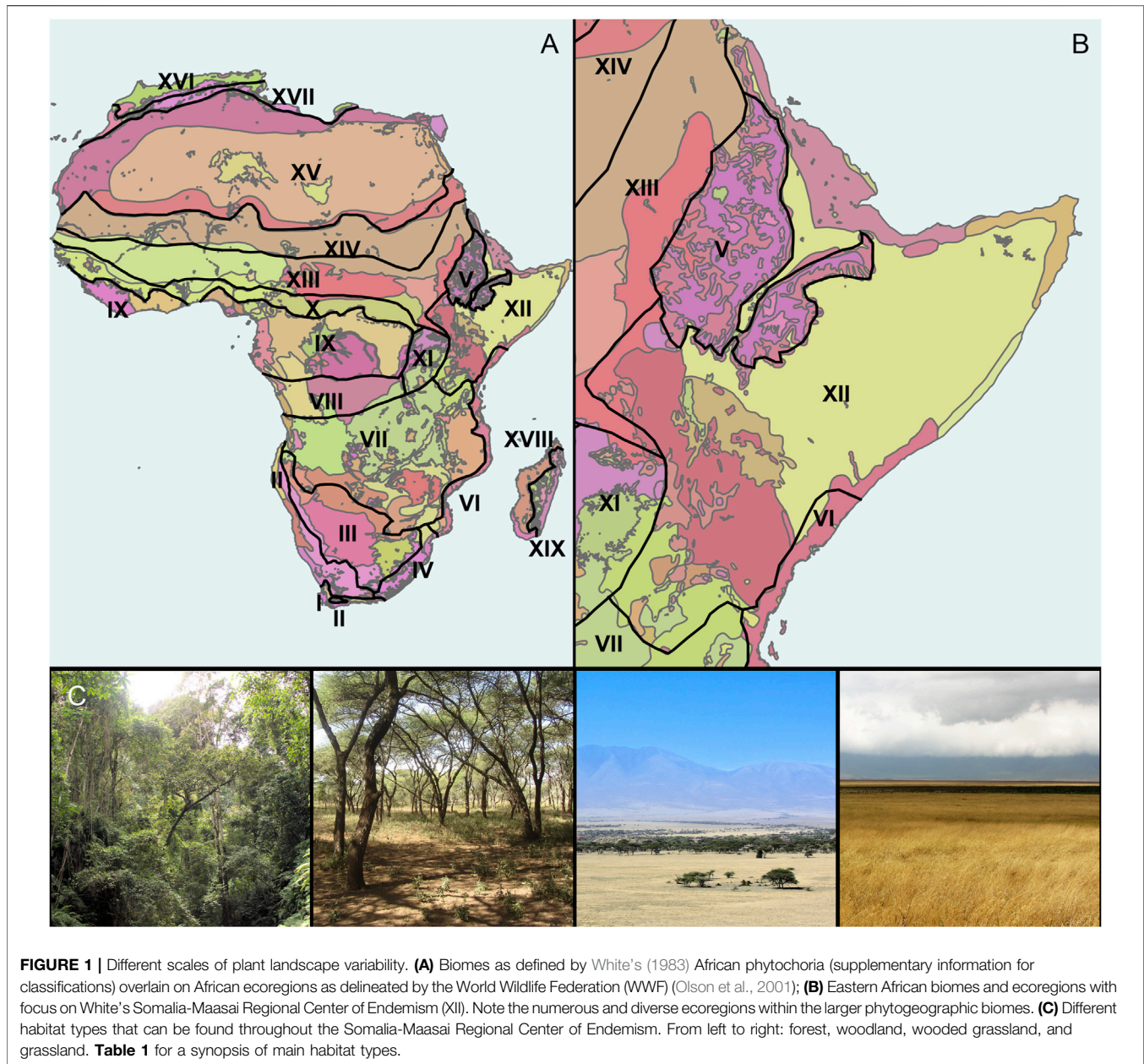
Yet, linking hominin landscape ecology and climate variability to technological, morphological, or behavioral changes remains challenging as clear cause-and-effect relationships between specific climatic events and major evolutionary occurrences are difficult to establish. This is often due to temporal and spatial gaps in paleoclimatic, paleoenvironmental, and archaeological records (Marean et al., 2015; Faith et al., 2019; Faith et al., 2021). Additionally, recent discoveries of the earliest stone tools (i.e., the Lomekwian) from Kenya dating to 3.3 Ma (Harmand et al., 2015), the earlier appearance of *H. erectus* in southern Africa at 2.0 Ma (Herries et al., 2020), and the likelihood that Acheulean biface shaping emerged gradually out of bifacial core reduction during the Oldowan (Duke et al., 2021) are not evidently linked with major climate and environmental events. Furthermore, Northern Hemisphere Glaciation was a gradual process, and a consistent stepwise transition toward greater aridity in Africa at ~2.8 Ma does not exist, with regional, often asynchronous, changes being observed in different parts of the continent (Trauth et al., 2021). Mammalian evolution is also not always directly linked to major climate shifts in a one-to-one manner as species adopt a variety of strategies, including mobility/migration, dietary, morphological, or cultural change, and the ongoing utilization of small microhabitats within a wider changing regional environmental context (Boutin and Lane, 2014; McCain and King, 2014; Figueirido et al., 2019; Stewart et al., 2021).

Indeed, particular caution must be adopted when studying paleoclimate and paleoecology within a human evolutionary framework, as hominin habitat-types are not always synchronous with changes in regional or global climate (Blumenthal et al., 2017; Groucutt, 2020; Faith et al., 2021; Trauth et al., 2021). That is, landscape response data (most commonly, records of vegetation change), are often used as a climate proxy even though it is well established that ecosystems do not necessarily exhibit a linear response to global or regional climate drivers (Holling, 1973; Bennett et al., 2021). Although difficult to identify archaeologically, we must also consider hominin agency, specifically the genus *Homo* in comparison to other hominins and primates, for its capacity to survive and adapt

to resource limited conditions and manipulate their environments. We know, for instance, that by least ~1.8 Ma (Gabunia et al., 2000; Zhu et al., 2008; Garcia et al., 2010; Ferring et al., 2011) and possibly ~2.1 Ma (Zhu et al., 2018), *Homo* had adapted to multiple climate zones and ecoregions within and beyond Africa, selected specific habitats within larger biomes, and was able to tolerate extreme climatological and ecological events without the need of sophisticated technology. In addition, Middle Pleistocene hominins modified their ecosystems, such as through fire use, which influenced local and regional ecologies, thus adding another dimension to vegetation change that is not entirely climate mediated (Gowlett, 2016; Petraglia, 2017; Thompson et al., 2021).

Until relatively recently, cross-disciplinary datasets in direct association with stratified archaeological and fossil assemblages were not specifically targeted when reconstructing hominin landscape environments or ecologies. “Off-site” (i.e., distal) lake and ocean cores have produced well-integrated, high-resolution reconstructions of the broad environmental context in which the genus *Homo* and its closest hominin relatives evolved, adapted, and experimented with novel technologies (Feakins et al., 2005; Feakins et al., 2007; Castañeda et al., 2009; Magill et al., 2013a; b; Uno K.T. et al., 2016; Tierney et al., 2017; Caley et al., 2018; Colcord et al., 2018; Lupien et al., 2018; Lupien et al., 2019; Lupien et al., 2020; Lupien et al., 2021). These data, however, are often derived from sources distal to hominin activity. Although we have long-term records that demonstrate changes in plant landscape composition (Feakins et al., 2005; Feakins et al., 2007; Feakins et al., 2013; Uno K. T. et al., 2016), they do not necessarily show the ecological subtleties and complexity that on-site (i.e., proximal) records can provide. Increasingly, however, phytolith and pollen records (Bonnefille, 1995; Barboni et al., 1999; Albert et al., 2006; Bamford et al., 2006; Bamford et al., 2008; Albert et al., 2009; Barboni et al., 2010; Rossouw and Scott, 2011; Albert and Bamford, 2012; Barboni, 2014; Albert et al., 2018; Itambu, 2019; Mercader et al., 2021; Stollhofen et al., 2021), as well as paleontological and stable isotope analyses (WoldeGabriel et al., 1994; Cerling et al., 1997; Pickford and Senut, 2001; Wynn, 2001; White et al., 2009b; WoldeGabriel et al., 2009; Prassack, 2010; Cerling et al., 2011; Kovarovic et al., 2013; Magill et al., 2013a; b; Quinn et al., 2013; Bibi and Kiessling, 2015; Bibi et al., 2018; Colcord et al., 2018; Pante and de la Torre, 2018; Prassack et al., 2018; Faith et al., 2019; Roberts et al., 2020; Sanders, 2020), have sought to track changes in landscapes occupied by Pleistocene hominins. The pursuit of more detailed data relating to hominin population resource use and microhabitat availability across space and time is beginning to provide more nuanced insights into the relationship between hominin morphologies and technologies and local-to-regional scale environmental change (Barboni et al., 2010; Blumenshine et al., 2012; Magill et al., 2015; Itambu, 2019; Patalano, 2019; Martin et al., 2021; Mercader et al., 2021).

This article reviews the potential role of microhabitat variability in human evolution by examining archaeological and paleoecological datasets that have revealed hominin morphological and technological adaptations to changing

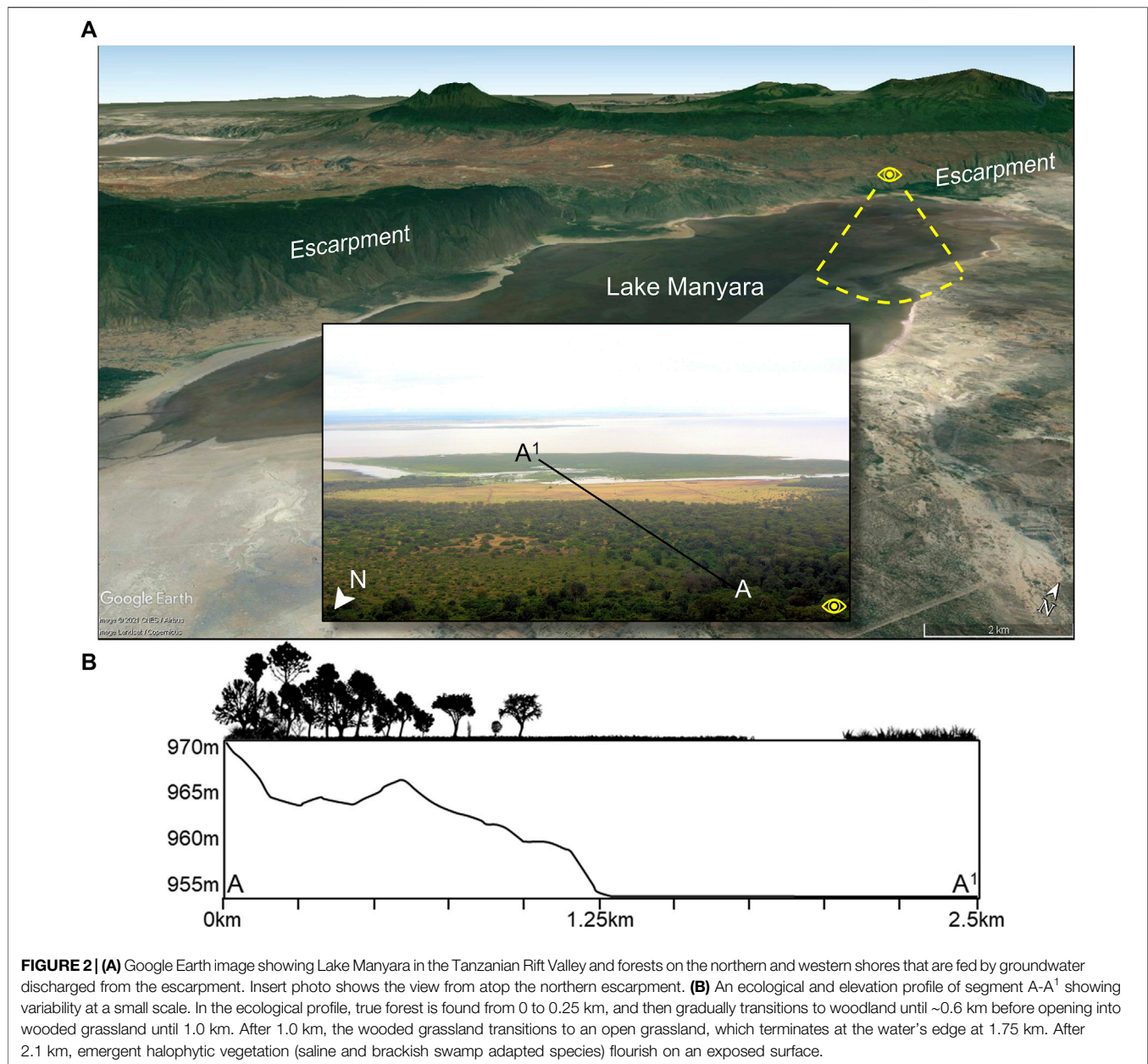


environments over time and space. We begin by defining microhabitat variability, and the differences between biomes, ecoregions, and habitats. We then present field and analytical research methods designed to identify microhabitat variability in the Pleistocene. This is followed by a review of the key prevailing climate and environmental hypotheses for human evolution, as well as issues related to landscape response data like the inherently non-linear attributes of some ecosystems. This is followed by case studies using three examples of microhabitat variability from Oldupai Gorge (formerly Olduvai) in Tanzania and the adaptability of *Homo* to distinct environmental settings. Finally, we propose a framework for utilizing diverse datasets compiled from multiple environmental proxy records as an analytical tool for evaluating hominin adaptability across

ecologically diverse landscapes and consider how to best factor a microhabitat variability framework into existing paleoclimatic, paleoenvironmental, and evolutionary models.

MICROHABITAT VARIABILITY

High spatial resolution and multi-proxy archaeological and paleoecological datasets are crucial for locally reconstructing climate drivers and biome- and intrabiome-scale ecological change. Such analyses are a necessary starting point for underpinning how climate-ecosystem feedbacks have influenced hominin evolution. We classify "microhabitats" as unique ecologically and geographically defined areas within larger



habitats (Figure 1, Figure 2). At the largest scale are “biomes,” which we identify using White’s (1983) description of extant African phytochoria, termed *Regional Centers of Endemism* (White, 1979). Nested within the biomes are various “ecoregions,” or relatively large areas of land containing a distinct assemblage of natural communities and species that share climatic and environmental conditions (Olson et al., 2001). The porosity and chemistry of soils, topography, groundwater sources, and edaphic conditions influence vegetation structure and floristic patterns to create distinct habitat and microhabitat assemblages inside each ecoregion (Sept, 2013). “Habitats” are areas covered by relatively uniform vegetation types within each ecoregion (Table 1), that represent major biotic zones and correlate with various climatic

indices such as rainfall seasonality, summer aridity, and minimum winter temperatures (Van Wyk and Smith, 2001). A “microhabitat” on the other hand, is a smaller but highly distinctive area that differs from encompassing habitat types in that it exhibits unique floristic conditions that can change at meter scales (Figure 2). While, on a spatial scale, these ecosystems might seem relatively unimportant, biotically they can be home to a variety of diverse flora and fauna, often exerting specific pressures on the evolution of morphology, feeding behaviors, and migratory patterns (Fjeldså and Lovett, 1997; Stewart et al., 2010; Sintayehu, 2018).

Microhabitat variability is exemplified best by mosaics, or where local geological, tectonic, microclimatic, and hydrological conditions and both natural and anthropogenic

TABLE 1 | Synopsis of main habitat types mentioned in the text. Adopted from White, 1983.

Forest	A continuous strand of trees at least 10 m tall with a closed, multistory, overlapping canopy. Woody plants dominate the biomass, and a shrub layer is normally present. The ground layer is usually sparse but may contain bryophytes, epiphytes, orchids, or mosses depending on moister availability
Woodland	Open stands of trees that are at least 8 m high, but no more than 20 m, with woody plants accounting for ~40% of the biomass over a field layer of grasses. Woodland canopies do not overlap extensively, but occasionally, stands of woodland have a closed canopy and thus a poorly developed grass layer
Bushland and thicket	Open stands of bushes, defined as woody, multi-stemmed plants usually 3–7 m tall with a main stem 10 cm or more in diameter, that cover >40% or more of the land. Bushes often flourish in rocky or stony substrates that are unfavorable to grasses. Thicket is a closed stand of bushes that are so densely interlocked that they form a nearly impenetrable obstacle that hinders movement
Shrubland	Stands of shrubs that vary in height from 0.1 to 2 m. Usually open or closed stands of shrubs occur where taller bushes and trees cannot grow because of low rainfall, extended drought periods, low temperatures, high rates of evapotranspiration, and oligotrophic or nutrient-poor soils
Grassland	Stretches of grasses and other herbs that develop when woody plant cover is <10%. African grasslands are structurally simple with woody species only occurring in specialized microhabitats that are dependent on the availability of moisture. Forbs also form an important component of grasslands and may contribute more in terms of biome species richness than do grass species
Wooded Grassland	Stretches of grasses and other herbs, with woody plant cover ranging from 10 to 40%. Woody plants are always scattered, but often grade into grassland or woodland

disturbances create well-defined patches of distinct plant communities that may offer unique food resources (Mucina and Rutherford, 2006). Gallery forests for example, are a key element within the Somalia-Maasai Regional Center of Endemism of eastern Africa (White, 1983), which consists of *Acacia-Commiphora* deciduous bushland and thicket, wooded grassland, edaphic grasslands, and other habitat types. Dense, fire-exclusionary gallery forests can grow proximal to abundant or permanent freshwater sources, including near rivers or groundwater aquifers. Thus, a particular combination of eco-hydrological conditions can permit the formation of highly diverse landscape mosaics over relatively small geographic distances (Mucina and Rutherford, 2006). Contributing to microhabitat variability is ecological diversity, which includes both alpha (α -diversity) and beta (β -diversity) diversity (Whittaker, 1960). Alpha diversity reflects that within a localized microhabitat, while β -diversity reflects that between different microhabitat types. Both α -diversity and β -diversity are determined by climatic conditions as well as the frequency of fires and other disturbances and a combination of slopes, aspect, soil depth and nutrients, moisture availability, age, and evolutionary history of the landscape (Geldenhuys, 1992; Mucina and Rutherford, 2006). The well-drained alluvial fans on the northwestern and western shores of Lake Manyara, Tanzania for example, support a “drought resilient” groundwater-fed evergreen forest that would otherwise not develop under the existing rainfall regime of 650 mm per year (Copeland, 2007; Barboni, 2014) (Figure 2). This forest is atypical of the Somalia-Maasai *Acacia-Commiphora* deciduous bushland and thicket and volcanic grasslands that abound in this region of Tanzania. Crucially, this forest supports key edible taxa that are relied upon by a range of fauna (such as chimpanzees in western Tanzania) like the Cape Mahogany (*Trichilia emetica*) and the Sycamore Fig (*Ficus sycomorus*) (Copeland, 2007 and references within).

Identifying Microhabitat Variability

Reconstructing microhabitat variability through archaeological or paleoecological proxies is, of course, difficult given the delimited nature of excavations or core retrieval and taphonomic limitations. Recent studies, however, have shown that it is possible to track microhabitat changes at spatial scales (Magill et al., 2015; Arráiz et al., 2017; Itambu, 2019; Patalano, 2019). Many archaeological and paleoanthropological sites permit well-defined, high-resolution temporal analyses, though few have had adjacent geological exposures that allow for analyses to be conducted at a high spatial resolution targeted as well. Oldupai Gorge in northern Tanzania, the Ain Béni Mathar-Guefaït basin in eastern Morocco, and even the Nihewan Basin in northern China are such examples where exposed sedimentary deposits allow for radiometric or magnetostratigraphic dating of fluvio-lacustrine sequences so that both temporal and spatial paleo-reconstructions are possible (Figure 3). The application of sequence stratigraphic methods to geologic exposures provides a time-layered framework that enables correlations between sedimentary units across facies boundaries (Uribelarra et al., 2017; Stanistreet et al., 2018). This also allows for the horizontal sampling of terrestrial sediments at and beyond archaeological sites, as well as across exposed sedimentary units along meter-, and when possible, kilometer-scale transects (Figure 3). The analyses of specific paleo-proxies (Table 2) collected in paleosol horizons can then help document spatial distributions in vegetation and provide an ecological context of such things as hominin foraging behavior or raw material procurement (Section 5).

Nevertheless, investigations into hominin resource use and microhabitat variability have largely been limited to Oldupai Gorge due to its number of documented archaeological sites, geographic extent, and well-defined stratigraphy (Barboni et al., 2010; Blumenschine et al., 2012; Magill et al., 2015; Itambu, 2019; Patalano, 2019; Mercader et al., 2021). Sampling at other paleoanthropological locations on the other hand, has mostly

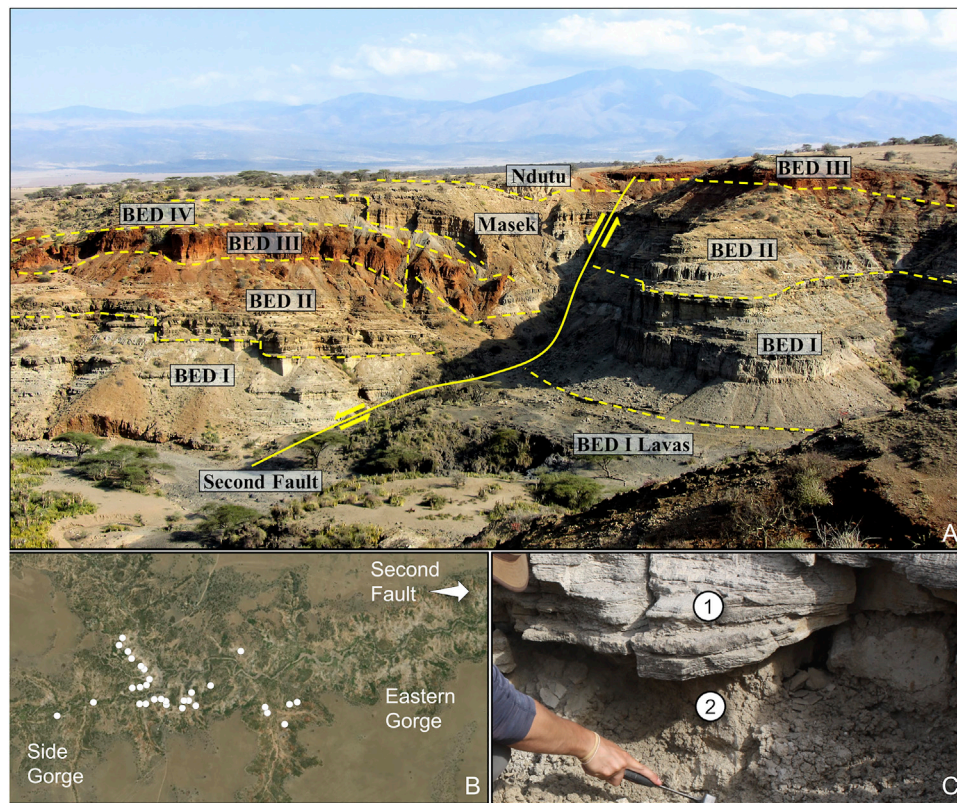


FIGURE 3 | Stratigraphic overview of Oldupai Gorge and landscape sampling for spatial habitat variability. **(A)** View of the Second Fault in the eastern part of the gorge and the displacement of the stratigraphic Beds. On the left (hanging wall), all beds except for Naisiusiu are exposed, while on the right (foot wall), only the Bed I Lavas and Beds I-III are visible. Exposure taken from the northern rim of the gorge facing south and encompasses ~600 m east to west. Photo by Robert Patalano. **(B)** Locations (white dots) around the main confluence of the gorge where clays in contact below Tuff IF were sampled for plant wax biomarkers and phytoliths (Itambu, 2019; Patalano, 2019). **(C)** Example in which both Tuff IF (1) and the clays in contact below the tuff (2) are exposed. Photo by Laura Tucker.

TABLE 2 | Main paleoecological proxies that can be used to study microhabitat variability.

	Pollen	Phytoliths	Plant waxes	Faunal isotopes
Benefits	Compositionally rich record of vegetation change Highest taxonomic resolution	Often abundant in paleosols Can track boundary between woodland and grassland	Ubiquitous in terrestrial and aquatic sediments Track photosynthetic pathway and changes in hydroclimate	Ratios track dietary preference Provide landscape-scale environmental signals
Drawbacks	Preservation contingent on anoxic conditions, usually in aquatic depositional settings Transport distance differs between taxa	Cannot reliably identify photosynthetic pathway or plant taxonomy, specifically at the species level	Production varies by taxonomic group Preservation depends on initial burial dynamics and diagenesis	Biased to feeding behavior Not diagnostic of hominin habitat preference

focused on proxy records collected in lake basin or ocean cores that track long-term climatic trends and regional environmental signals (Faith et al., 2021). Classifying paleo-microhabitats is also contingent on the taphonomy of environmental proxies (Table 2). Diverse faunal assemblages can suggest the juxtaposition of distinct microhabitats (Kovarovic et al., 2013), but can be skewed by niche exploitation of specific species by hominins or the disproportional preservation and dominance of some species [e.g., very large mammals (≥ 180 kg)] in fauna collections over other [e.g., small mammals ($< 1,000$ g)] (Faith

et al., 2019). Biogenic silica, pollen, and plant wax biomarkers (Godwin, 1934; Faegri and Iversen, 1989; Piperno, 2006; Sachse et al., 2012; Diefendorf and Freimuth, 2017; Cabanes, 2020; Patalano et al., 2021), are three additional proxies most often applied for plant landscape reconstructions (Table 2), and when used effectively, have the potential to produce a clear ecological context into which hominin behavior can be interpreted (e.g., Mercader et al., 2021). By taking a multi-proxy approach to studying non-analog ecosystems and microhabitat variability, it is possible to overcome some of the problems inherent with

TABLE 3 | Synthesis of selected environmental hypotheses for human evolution.

Hypothesis	Type	Environmental setting	Evolutionary outcome	Drawback	References
Savanna	Habitat specific	Transition from closed forest to open grassland	Bipedalism, tool use, encephalization, etc.	Hominin landscapes were ecologically diverse with multiple habitat types	Dart (1925); Washburn (1960); Wilson (1979); Wolpoff (1980); Coppens (1994)
East side story	Habitat specific	Wet, forested west/central Africa vs. dry, open eastern Africa	Split between <i>Pan</i> and <i>Homo</i> from last common ancestor	Based on the assumption that hominin evolution only occurred in eastern Africa	
Turnover pulse	Climate variability	Rapid phases of aridity and limited resources	Extinction and speciation	No solid evidence for rapid ecological and evolutionary changes in the eastern African fossil record	Vrba (1985); Vrba (1995a); Vrba (1995b); Vrba (2007)
Variability selection	Climate variability	Trends toward drier and more variable climate resulting in unpredictable resource base	Heritable traits that enhance adaptive versatility favored over those that thrive in stable environments	Assumes linear driver-response between climate change and hominin ecosystem change	Potts (1996); Potts (1998b); Potts (2013)
Pulsed climate variability	Climate variability	Short periods of extreme climate variability and rapid landscape reorganization	Hominin speciation, encephalization, and dispersals out of Africa	Does not account for hominin localities or habitats beyond the East African Rift Valley	Maslin et al. (2014)
Red queen	Productive stability	Stable, predictable, resource rich environments	Competition amongst species leading to fitness optimum and evolution	Ignores importance of abiotic factors and may only operate at the population level	Van Valen, (1973)
Chase red queen	Productive stability	Stable, predictable, resource rich environments	Cladogenesis (typically amongst populations)	Has been difficult to show in extinct taxa	Strotz et al. (2018)
Microhabitat variability	Ecological variability	Diverse and varied with ample resource opportunities	Successful adaptability of <i>Homo</i> to environmentally complex landscapes	Few paleoanthropological localities allow for testing spatial variability	—

undertaking regional climate-ecosystem comparisons for human origins studies (Faith et al., 2019; Faith et al., 2021).

ENVIRONMENTAL AND CLIMATE VARIABILITY AND HUMAN EVOLUTION

The evolutionary significance of climatic and environmental variability has been reviewed elsewhere within the context of human origins (Vrba et al., 1989; Potts, 1996; 1998a; b; Vrba, 2007; Maslin and Trauth, 2009; Potts, 2013; Maslin et al., 2015; Faith et al., 2021). Early explanations of human evolution focused on intrinsic stimuli whereby a simple transition from one habitat type to another (forest to grassland, for example) set the stage for speciation or specific hominin characteristics like bipedalism and tool use (Dart, 1925; Washburn, 1960; Wilson, 1979; Wolpoff, 1980; Coppens, 1994). While these *Habitat Specific Hypotheses* have, for the most part, been replaced, their assumptions often persist in evolutionary discourse (Table 3). Generally, these hypotheses stipulate that the transition from closed woodlands to open grasslands underpinned the development of meat-eating, hunting, brain enlargement, fire use, food distribution, complex sociality, and even language (review in Potts, 2013).

Laporte and Zihlman (1983) were early proponents for the impact of environmental change on driving African mammalian evolution (including hominins) by proposing that adaptive changes were a response to changing environments caused by global cooling or orogeny, or as hominins migrated into new habitats. This has since resulted in multiple climate variability hypotheses that link changes in climate to environmental reorganization and subsequent speciation and extinction

events, species' adaptive versatility, and the selection of behavioral and morphological mechanisms that enhance adaptive fitness (Table 3). For instance, the appearance of *Homo* and *Paranthropus* around 2.5 Ma was proposed to have followed climate pulses caused by Northern Hemisphere glacial intensification and the closing of the Isthmus of Panama (Vrba et al., 1989; Vrba, 1995a; b). We now know, however, that there is even earlier evidence of *Homo* around 2.8 Ma (Villmoare et al., 2015), and possibly as early as 3.3 Ma, (Püschel et al., 2021), and there was no pulse towards greater aridity in Africa at the time (Trauth et al., 2021). On the other hand, increased ecological resource variability (Potts et al., 2020) is considered a major factor in a species' adaptive versatility specifically in unstable, unpredictable, or unfamiliar environments, and there is now more compelling evidence for hominin evolutionary events during periods of highly variable eastern African climate shifting from very-dry and very-wet conditions between 5.0 and 0.2 Ma (Trauth et al., 2005; Maslin et al., 2013; Maslin et al., 2014; Potts et al., 2020; Lupien et al., 2021).

In contrast to these hypotheses centered on upheaval and change, some treatises have argued that climatic stability may have been important for driving hominin evolution as species must adapt and evolve in competition with other evolving species (Van Valen, 1973; Strotz et al., 2018). In these (Table 3), highly productive and stable environments lead to competition among species resulting in directional selection as they move toward fitness optimum when striving to gain a competitive advantage over others (Brockhurst et al., 2014). As cladogenesis can lead to populations deviating from their species and the possibility of a descendant evolving while its ancestor persists, there is thus a link between microevolutionary processes and macroevolutionary

patterns (Strotz et al., 2018). *P. boisei*, *H. erectus*, *H. habilis* and *H. rudolfensis* were all present at Koobi Fora during the maximum extent of Paleo-Lake Lorennyang (1.9–1.8 Ma), when resource availability would have been highest, resulting in these hominins co-evolving in competition with each other (Maslin et al., 2015). Additionally, *Au. sediba*, *P. robustus*, and *H. erectus* were contemporaneous in South Africa between 2.04 and 1.95 Ma (Berger et al., 2008; Herries et al., 2020), coinciding with substantial changes in South African ecosystems that may have placed selective pressures on *Australopithecus*, leading to divergent *Homo* and *Paranthropus* lineages (Ledogar et al., 2016; Joannes-Boyau et al., 2019).

ECOSYSTEM RESILIENCE IN FACE OF CLIMATE CHANGE

Disentangling the influence of climate changes on plant landscapes and impacts on resource availability is a fundamental, yet often overlooked, stepping-stone for linking climate drivers to human behavioral change, evolution, and migration patterns. This is an essential element for validation of the variability hypotheses given that they all mandate a degree of environmental determinism (e.g., Faith et al., 2021). Yet historically, paleoecological and paleoclimatic records have often been conflated (e.g., Morrison and Hamilton, 1974), an approach often necessitated by cost, access, and methodological constraints. While linear driver-response assumptions may be viable for climatically sensitive habitats such as tropical montane settings, they may overlook the inherently non-linear attributes of ecosystems (Holling, 1973; Hirota et al., 2011; Willis et al., 2013; Seddon, 2021). Thus, an interpretation of a stable climate exclusively drawing on paleoecological data extracted from a climatically resilient ecosystem would be entirely misconstrued (Hamilton et al., 2020). Equally problematic is an assumption of extreme climate change from ecological data showing a catastrophic ecological state shift in response to a relatively minor, potentially non-climatic disturbance (Hirota et al., 2011). This emphasizes the importance of producing independent records of climatic and non-climatic stressors and landscape response data prior to making interpretations of hominin behavior from the archaeological record.

From a climate perspective, the progressive formation of the East African Rift System (EARS) after 12 Ma increased aridity in eastern Africa as wind patterns became less zonal, reducing available moisture particularly on the leeward sides of uplifted regions (Sepulchre et al., 2006; Hardt et al., 2015). Tectonic activity also helped create distinctive and topographically complex landscapes and geographical barriers that hominins had to successfully navigate (King and Bailey, 2006). Evidence from soil carbonates (Wynn, 2001; Levin et al., 2004; Wynn, 2004; Levin et al., 2011; Quade and Levin, 2013) and pollen and plant wax biomarkers (Feakins et al., 2005; Feakins et al., 2007; Feakins et al., 2013) illustrate a progressive proliferation of C_4 plants beginning at approximately 10 Ma, presumably in response to increased aridity following rifting (deMenocal, 2004). Grass pollen and plant wax biomarkers from marine cores in the

Gulf of Aden (Feakins et al., 2013) and the Somali Basin (Uno K. T. et al., 2016) show that C_3 grasslands had actually expanded in eastern Africa by 12 Ma but from 10 Ma onwards, were steadily replaced by C_4 plants (Feakins et al., 2007; Uno K. T. et al., 2016), though this was not a gradual process (Magill et al., 2013a; b; Colcord et al., 2018; Lupien et al., 2019).

Changes in northeastern African flora have also been attributed to variability in orbital precession (Feakins et al., 2005; Feakins et al., 2007; Maslin and Trauth, 2009; Magill et al., 2013b; Feakins et al., 2013; Uno K. T. et al., 2016; Lupien et al., 2018). Precession, with an average periodicity of ~23,000 years, may have influenced human evolution and adaptability by controlling local water availability, biome diversification, and key speciation and dispersal events (Maslin and Trauth, 2009; Potts, 2013). Environmental variability may have also increased the adaptive versatility of hominins and their capacity to adjust to new habitats (Potts, 2013). The timing and nature of changes in hydrology and vegetation cover and the relationship to hominin species turnover (Feakins et al., 2007; Lupien et al., 2018), the appearance of new stone tool technologies (Lupien et al., 2020), the ability to control fire (Collins et al., 2017; Brittingham et al., 2019), and hominin dispersals out of Africa (Castañeda et al., 2009; Tierney et al., 2017) have all been viewed in light of orbital forcing and environmental variability. In southeastern Africa, rapidly fluctuating wet-dry cycles between approximately 2.2 Ma to 2.0 Ma likely contributed to the local extinction of *Australopithecus* and *Paranthropus* due to habitat marginalization (Caley et al., 2018), at a time when the genus *Homo* was emerging prominently in Africa (Antón, 2003; Plummer et al., 2009; Herries et al., 2020).

On shorter timescales, the Intertropical Convergence Zone (ITCZ) dictates the position of African and Indian Ocean Monsoons and controls the seasonal distribution of precipitation across Africa (Nicholson, 1996). Driven by solar insolation, the ITCZ produces singular rainy seasons in many parts of the continent, but it is difficult to simply attribute African precipitation cycles directly to incoming solar radiation (Yang et al., 2015), as African hydroclimate is modulated by influences from both the West African and Indian Ocean monsoons, the Walker Circulation, topography, and anomalies of ocean sea-surface temperatures, all of which can cause unimodal to trimodal distributions of rainfall across of the continent (Nicholson, 1993, 1996; Williams et al., 2012; Yang et al., 2015; Parhi et al., 2016; Ummenhofer et al., 2018; Schaebitz et al., 2021). In eastern Africa for example, the region's aridity has been attributed to the Turkana low-level jet (Nicholson, 2016) and orography (Christensen and Kanikicharla, 2013) even though there is a bimodal annual cycle of precipitation. Continental rainfall distribution is also sensitive to changes in the El Niño Southern Oscillation (ENSO) (Nicholson and Selato, 2000; Pausata et al., 2017), originating from Pacific sea surface temperature anomalies (Kaboth-Bahr et al., 2021). Changes in ENSO influence east-west and equatorial-southern moisture gradients across Africa (Nicholson and Selato, 2000; Nash et al., 2016; de Oliveira et al., 2018), such that when humid condition prevail in eastern or equatorial Africa, arid conditions persist in

western or southern Africa (Nicholson, 1996; Kaboth-Bahr et al., 2021).

African plant landscapes, and forests in particular, are unique in that they recover faster after disturbances and appear to be more resistant to drought compared to other tropical habitats, such as those in South America or Southeast Asia (Willis et al., 2013; Cole et al., 2014; Bennett et al., 2021). This drought-resistance may be due to the relatively dry contemporary conditions across the continent (Malhi et al., 2004) as well as the biogeographic history and diversification of drought-adapted species (Parmentier et al., 2007). As African climate has oscillated between wetter and drier conditions, modern plant biomes may have developed drought-tolerance over time due to the loss of mesic-adapted species (Pennington et al., 2009). If, for example, humid lowland tropical African forests are more resistant to short-term extreme climate anomalies today, it is possible that moisture availability across Africa (e.g., paleo-ENSO effects) may not have had a large role in governing the distribution of vegetation communities or plant landscape structure at shorter timescales during the Pleistocene (Bennett et al., 2021). There is also non-linearity in both the spatial and temporal response of African vegetation to specific climatic drivers. Understanding these differences is important for determining spatial patterns of resilience and the sustainability of ecosystems in relation to climate changes (Willis et al., 2013).

Alternatively, hominin ecosystem engineering, especially intentional fire manipulation by *H. sapiens*, is an aspect of vegetation change that is not entirely climate mediated but may have had a significant influence on plant community composition and structure (Gowlett, 2016; Petraglia, 2017; Thompson et al., 2021). Controlled fire use is apparent in the archaeological record prior to the Middle Stone Age (Glikson, 2013; Gowlett, 2016), and both archaeological and ethnographic evidence indicate deliberate landscape modification through controlled burning to maintain mosaic landscapes and as a subsistence-related strategy (White, 2013; Scherjon et al., 2015; Petraglia, 2017; Bliege Bird et al., 2020; Thompson et al., 2021). This also suggests that controlled and manipulated fire may have had a pronounced effect on Pleistocene environments (Archibald et al., 2012), with Middle Pleistocene hominins burning landscapes to create resource-rich microhabitats that provided populations with abundant gatherable plants and ecological settings appealing to animal prey species (Haws, 2012; Thompson et al., 2021). Reconstructing paleoenvironments through a microhabitat variability framework can therefore help to understand the impact of hominin ecosystem modification on plant landscapes, especially when non-linearity and spatial patterns of resilience and climate drivers are also considered.

MICROHABITAT VARIABILITY AND HUMAN EVOLUTION

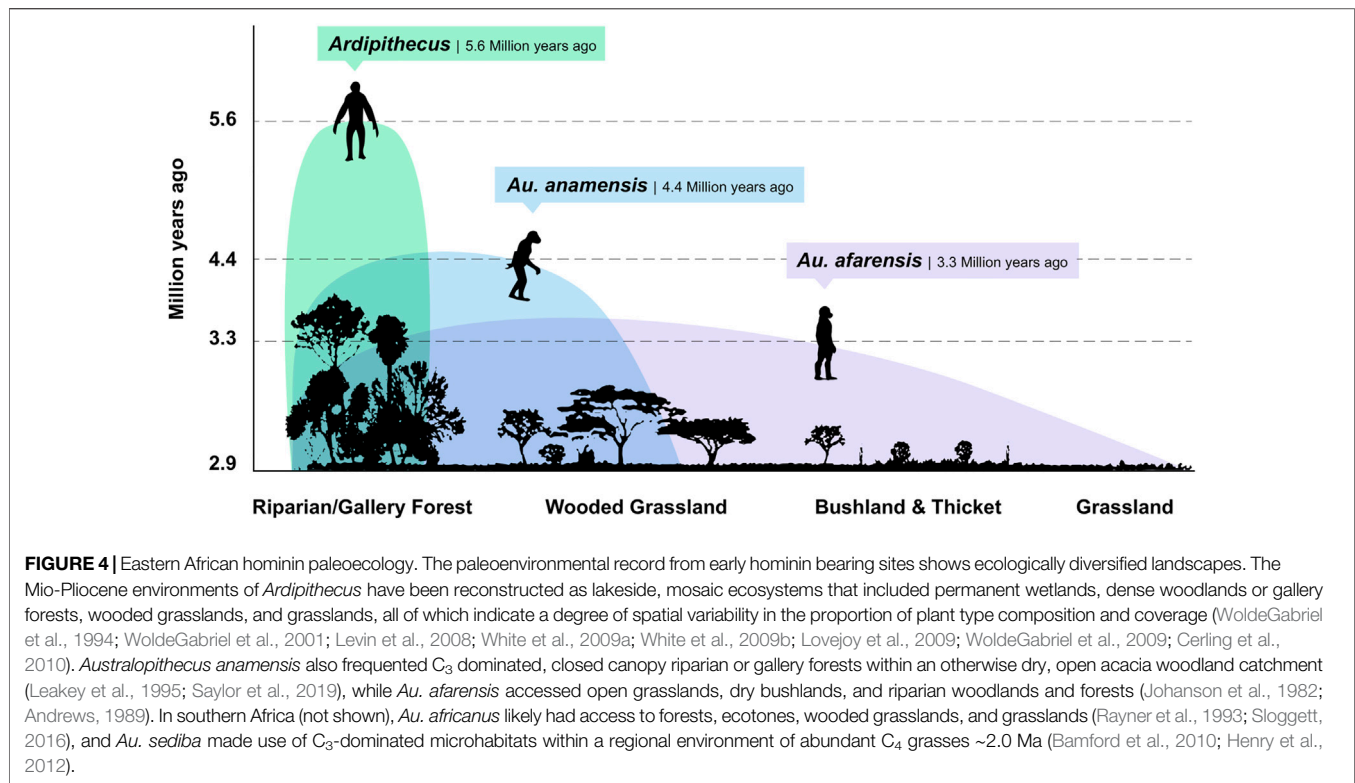
By two million years ago, there is an apparent increase in the body mass of *Homo* (Pontzer, 2012; Antón et al., 2014), which in turn is related to its wider geographic distribution compared to other

hominins (Antón, 2003) and an increase in energy expenditure (Aiello and Key, 2002; Aiello and Wells, 2002). Additionally, there was a shift in the archaeological record from assemblages of low-density artifact scatters in narrower depositional contexts to denser concentrations of archaeological material in a broader array of habitat settings (Plummer and Finestone, 2018). Although earlier hominins had access to a wide array of habitat types (Figure 4), *Homo* excelled in the successful exploitation of resources from greater ecological contexts. In eastern Africa for example, greater tool use possibly allowed hominins to adapt to microhabitat variability and ecological instability, as evident in the occupation of a broad spectrum of habitats ranging from open grasslands to riparian forests. At Kanjera South, on the Homa Peninsula in Kenya, hominins exhibited comparatively complex land use and toolmaking behaviors as raw materials were transported from over 10 km (Braun et al., 2008a; Braun et al., 2008b; Braun et al., 2009a; Braun et al., 2009b; Braun and Plummer, 2013). Tools were employed to process a diverse range of resources including animal tissue and underground storage organs and woody and herbaceous plants (Ferraro et al., 2013; Lemorini et al., 2014; Lemorini et al., 2019).

Microhabitat Variability at Oldupai Gorge: A Case Study

As an “archaeosphere” representing the paleoanthropological record of broader eastern Africa, Oldupai Gorge (formerly Olduvai Gorge) presents an interesting opportunity to explore microhabitat variability across both temporal and spatial scales using multiple paleoecological proxies collected in archaeological and geological horizons (Figure 3, Supplementary Figure S1). Spatial geomorphological, sedimentological, stratigraphic, and geometric analyses are made possible by Oldupai’s well-defined Beds: I-IV (2.038 ± 0.005 – 0.6 Ma), Masek (600,000–400,000), Ndutu (400,000–32,000), and Naisiusiu ($17,550 \pm 1,000$ – $10,400 \pm 600$ BP) (Leakey, 1971; Hay, 1976; Deino, 2012; Domínguez-Rodrigo et al., 2013; Diez-Martín et al., 2015). In fact, these beds and marker tuffs, which are exposed for ~25 km throughout the eastern and western gorges, have made it possible to correlate paleoecological and archaeological datasets across time and space, highlighting the evolution of *Homo* within a diverse, variable landscape (Cavallo and Blumenschine, 1989; Sikes, 1994; Blumenschine et al., 2012; Uribelarra et al., 2014; Uribelarra et al., 2017; Stanistreet et al., 2018).

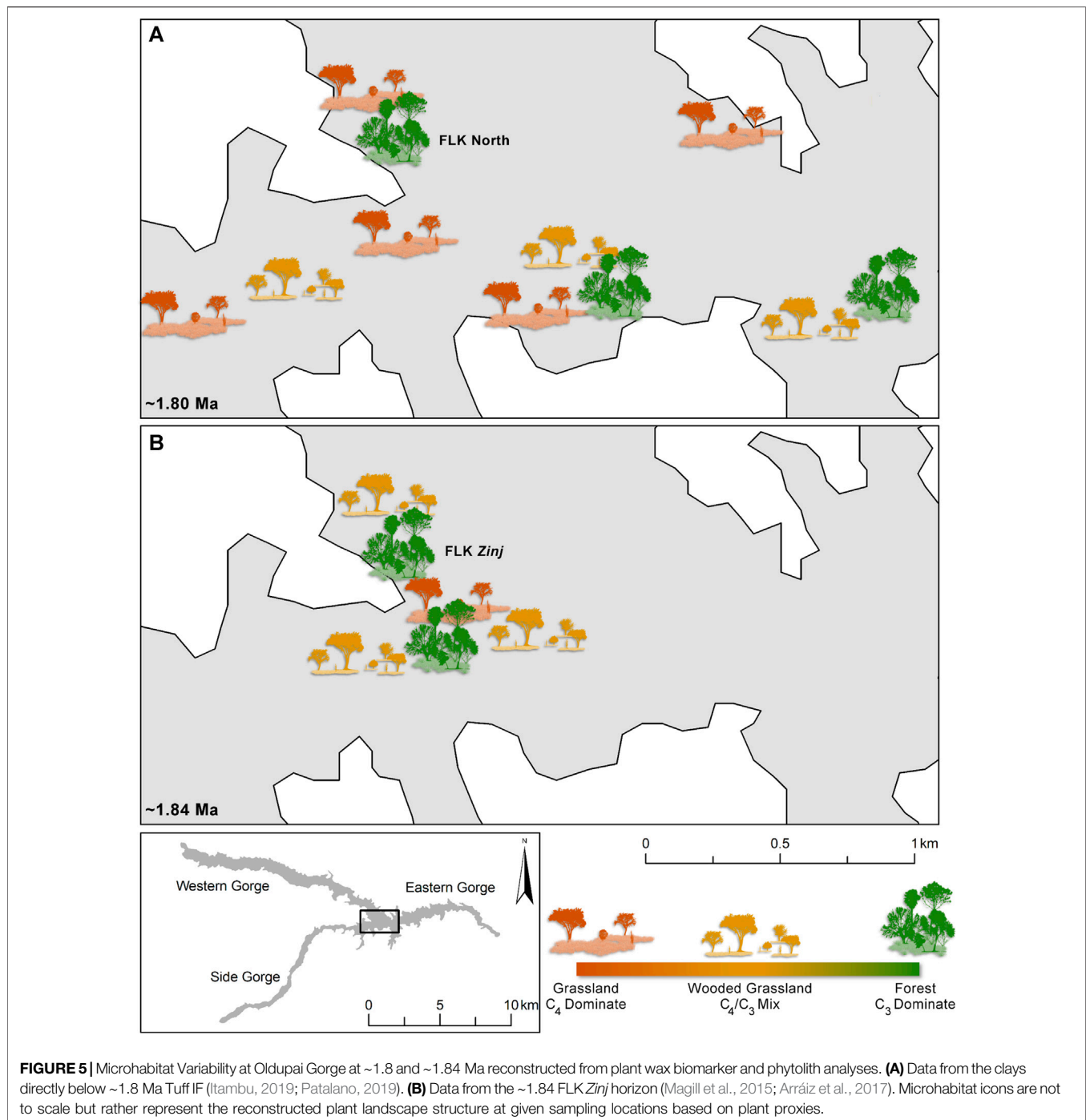
At the Ewass Oldupa site, where the earliest evidence of the Oldowan is found at Oldupai Gorge (Mercader et al., 2021), hominins used a homogenous toolset within emerging landscapes and volcanically-disturbed habitats multiple times over 235,000 years. The Oldowan assemblage consists of some raw material sourced from up to ~12 km away and shows technological adaptation to major geomorphic and ecological transitions, whereby stone tool use permitted provisioning across ecologically diverse and complex environments over time and space. Tool use allowed for a more generalist strategy in acquiring plant food resources within a rapidly changing plant landscape that ranged from fern meadows to woodland mosaics, naturally burned landscapes, lakeside woodland/palm



groves, and hyper-xeric steppes. This generalist strategy and ability to use emerging landscapes, a finding that is unique for *Homo* ~ 2.0 Ma, depicts complex behavior among early Pleistocene hominins. Early evidence of this environmental response suggests that fundamental aspects of human adaptability was not solely connected to our species' origin (Potts et al., 2020), but rather by the time of our genus' origin and likely played a major role in *Homo*'s ability to expand within and beyond Africa.

Perhaps the most well-known locality at Oldupai is the Frida Leakey Korongo (FLK) site, as it was here at "Level 22" (better known as FLK *Zinj*) that Mary Leakey discovered *P. boisei* in 1959 (Leakey, 1959). This level, situated between Tuffs IB and IC (**Supplementary Figure S1**), was interpreted as an occupation or living floor (Leakey, 1959; Leakey, 1971), where hominins made stone tools to butcher mammals from nearby habitats (Bunn and Kroll, 1986; Blumenschine, 1995). Situated in uppermost Bed I and only ~100 m north of FLK *Zinj* is FLK North, one of the richest Pleistocene archaeological deposits known (Leakey, 1971; Domínguez-Rodrigo et al., 2010). FLK N is a 3.0 m, 15,000-years sequence in Upper Bed I subdivided into nine archaeological units dated between 1.803 Ma and 1.818 Ma (Deino, 2012). The marker tuffs that cap each site, and the organic rich silty-waxy clays directly in contact below the tuffs, are observable in exposures for more than 2 km throughout the main confluence of the gorge (**Figure 3**). These organic-rich clays were deposited on the alluvial fans and floodplains surrounding paleo-Lake Oldupai and have been the focus of recent paleoecological, microhabitat variability studies.

There is evidence from plant wax biomarkers (Magill et al., 2015; Patalano, 2019) and phytoliths (Barboni et al., 2010; Blumenschine et al., 2012; Arráiz et al., 2017; Itambu, 2019), collected from organic rich clays directly in contact with both Tuff IC and Tuff IF, for ecologically diverse hominin microhabitats throughout the Oldupai depositional basin (**Figure 3**, **Figure 5**). A combination of plant wax biomarkers and their stable carbon isotopes, phenol derivatives of lignin which distinguishes woody from herbaceous plants, fern and sedge biomarkers that demarcate wetlands, and phytoliths revealed the geographic distribution of different microhabitats across the FLK *Zinj* paleo-landscape (Magill et al., 2015; Arráiz et al., 2017). Abrupt changes from wetland vegetation, to dense C₃ woody coverage, to open C₄ grassland were identified at meter-level scales, showing that FLK *Zinj* was a forest microhabitat adjacent to a wetland situated within a greater grassland catchment (Magill et al., 2015). Compounded with the phytolith results, which are dominated by woody morphotypes and supported by grass, sedge, and palm types (Arráiz et al., 2017), both datasets indicate relatively wet and wooded microhabitats across the FLK *Zinj* landscape, situated within a catchment dominated by arid-adapted C₄ species. Additionally, plant wax carbon and hydrogen isotopes and biogenic silica also show that C₃ plants dominated the archaeological assemblage at FLK N (Itambu, 2019; Patalano, 2019). Phytolith and plant wax data from the clays directly below Tuff IF indicate that at the top of Bed I, Oldupai's landscape was variable mosaic with areas of dense vegetation and abundant fresh water (e.g., FLK N), *Typha* dominated wetlands, open grassland, and ecotones (**Figure 5**).



Interpreted as a woodland or even a true forest, the reconstructed C₃ environment at FLK N suggests that it may have been similar to the dense evergreen forest that now flourishes near freshwater springs percolating out of the rift escarpment on the northwestern and western shores of Lake Manyara.

The archaeology and paleontology of each site indicate that hominins butchered animals at FLK Zinj (Leakey, 1971; Blumenschine, 1995; Dominguez Rodrigo, 1997; Domínguez-Rodrigo and Barba, 2007; Domínguez-Rodrigo et al., 2014),

but processed hard-shelled nuts and fruits at FLK N (Domínguez-Rodrigo et al., 2007a; Diez-Martín et al., 2010; Domínguez-Rodrigo et al., 2010). Apart from the FLK Zinj Level 22 and David's Site (DS) (Domínguez-Rodrigo et al., 2017a), no other Bed I site provides evidence for access and the direct consumption of animals by hominins (Domínguez-Rodrigo et al., 2007b; Domínguez-Rodrigo et al., 2017b). That is, all other sites seemingly involved the use of Oldowan tools for plant processing (cf. Blumenschine, 1995). Woody vegetation

patches may have been the incentive that enticed hominins to use FLK Zinj and FLK N as focal points on the landscape to process both plant and animal foodstuffs acquired within the microhabitats that developed across Oldupai's basin.

EXPANDING THE MICROHABITAT VARIABILITY FRAMEWORK

Over the past two decades, spatial paleoecological analyses have allowed us to better understand the ways in which hominins adapted to microhabitat variability across space and time. Others have brought attention to the role microhabitat variability played in creating potentially resource-rich habitat types and opportunities for niche diversification and specialization amongst hominins (Stern, 1993; Foley, 1995; Cachel and Harris, 1998; King and Bailey, 2006; Reynolds et al., 2015). Higher spatial resolution environmental proxy data and more-precise dating techniques (Herries et al., 2020; Martin et al., 2021), even demonstrate the influence of microhabitat variability in shaping hominin evolutionary biology and anatomy. Although the focus has been on early *Homo* from around 2.0 Ma and at Oldupai Gorge, morphological differences between *P. robustus* from Drimolen and Swartkrans in South Africa, which are only ~6 km apart, represent highly resolved evidence for microevolutionary change associated with ecological variability across a short time frame and restricted geography (Martin et al., 2021). Differences in mandibular morphology between specimens from each location developed as a dietary adaptation to a marginal ecological setting. That is, the slightly younger but more robust Swartkrans *P. robustus* exhibit a more efficient bite force, likely representing a microevolutionary change within this population due to a dietary shift toward foods that were mechanically challenging to process (Sponheimer et al., 2006). This coincided with a reduction in ecological productivity following increased aridity and small-scale microhabitat reorganizations (Caley et al., 2018).

The Oldupai case study highlights how global and regional climate, tectonic and sudden geomorphological activity, and hydrogeography all contribute to spatially variable, often ecologically diverse and environmentally complex biomes, ecoregions, habitats, and microhabitats. Based on the available evidence, the ability of the genus *Homo* to adapt and thrive across regions of both high and low ecological diversity, as well as within ecosystems that change drastically, was in place by at least 2.0 Ma and likely assisted in technological developments and dispersals within and beyond Africa later in time. For instance, *H. sapiens*' successful ability to innovate under decreased resource predictability was cultivated by an evolutionary history of navigating complex and diverse ecological transitions. In the Olorgesailie basin of Kenya, the onset of the eastern African Middle Stone Age (MSA) is tied to *H. sapiens* behavioral and technological adaptation to habitat and resource variability (Potts et al., 2020). Between 400 and 320 Ka, dynamic landscape change through space and time (triggered by geologic, climatic, and ecological factors) likely led to lower resource reliability and may have necessitated that *H. sapiens* adopt MSA types of

stone tool technology as a hunting innovation (Potts et al., 2020), specifically as distinct ecological zones developed over a distance of less than 20 km following increases in Middle-to-Late-Pleistocene aridification and environmental variability (Owen et al., 2018).

By filling a “generalist specialist” niche, *Homo* and especially *H. sapiens*, excelled at adapting to environmental extremes and exploiting microhabitat variability across deserts, at high altitudes and latitudes, and within tropical rainforests, was able to successfully innovate under periods of decreased resource predictability (e.g., Potts et al., 2020), and construct their own environments (e.g., Thompson et al., 2021). As this ability to adapt and thrive in dynamic environments was already well-established in *Homo*, the addition of unique behavior like complex ecological knowledge and plant landscape modification and construction, eventually allowed *H. sapiens* to occupy of a wide diversity of ecological settings across the majority of the Earth's continents (review in Roberts and Stewart, 2018).

The microhabitat variability framework suggests that as African landscapes were impacted spatially by tectonic activity and hydrogeology, and temporally by orbital forcing and rainfall seasonality, the flexibility of *Homo* was likely beneficial in unstable, unpredictable, or unfamiliar environments. As tool innovation and use, specifically after 2.0 Ma, allowed for a more generalist strategy in acquiring plant and animal food resources across diverse and rapidly changing landscapes, the adaptive versatility of *Homo* and the capacity to adjust to new habitat types may have helped to withstand periods of extreme climate variability throughout the Pleistocene. There are numerous hypotheses regarding climatic variability driving hominin evolution and the eventual appearance and dispersal of our species (Table 3). However, there has been less consideration of ecological variability across space, largely due to sampling and methodological issues (also Faith et al., 2021). With new, transdisciplinary approaches toward reconstructing hominin environments directly on-site and across archaeological and geological horizons, we can address and test the following research questions:

- Did Pliocene and Pleistocene hominins rely on oases of woodland/forest habitats within wider grassland ecoregions? If so, to what extent and for what purpose (e.g., protection, food)?
- Did dispersals of hominins simply occur when larger ecoregions expanded (e.g., “savannah” corridors (Dennell and Roebroeks, 2005))?
- On the other hand, did geographic ecological variability always play a role in hominin dispersals first across Africa and then beyond?
- How can we better factor the microhabitat variability framework into paleoclimatic, paleoenvironmental, and evolutionary models? That is, can we go beyond the natural selection and speciation models that use distal proxy records to compare climate windows to biome and ecoregion changes and the ensuing influence on genetic variability and human evolution?

To tackle these questions, future research designs should consider correlating and sampling terrestrial sediments from archaeological and geological horizons to collect and analyze such environmental proxies as outlined in **Table 2**. This would involve identifying geologic strata and their geographic extent, collecting sediments from correlated deposits, testing organic preservation, and then paleoenvironmental reconstruction through proxy analyses. By understanding the spatial variability of environments and locations of concentrated archaeological assemblages, we can then better interpret hominin land-use patterns and activity within a regional and global climatic context to discern the ways in which *Homo* adapted to microhabitat variability over time and space.

CONCLUSION

Microhabitat variability provides a framework within which to understand the adaptability of hominins across spatially and temporally changing, sometimes rapidly, plant landscapes. Because members of the genus *Homo* were already adept at exploiting diverse food-types from multiple habitats including disturbed and emerging environments by 2.0 Ma, they successfully navigated ecosystem reorganization during pulses of climate instability throughout the Pleistocene. By incorporating paleoecological analyses for studying microhabitat variability in future paleoanthropological research, we can better interpret the evolutionary importance of climatic and non-climatic stressors and plant landscape responses to then validate or refute the habitat specific or variability hypotheses.

A microhabitat variability approach incorporates evidence for adaptations involving tool use, demonstrated by Oldowan hominins from Oldupai, high-resolution environmental proxy evidence for meter-scale changes in hominin landscape ecology, and field and laboratory methodologies for identifying patches of distinct plant communities that may have offered unique food resources and shelter. With research designs that focus on exploring and understanding hominin microhabitat variability, we can uncover further information relating to major adaptive morphological, technological, and cultural features that have not been fully addressed by human evolution environmental hypotheses. This approach, therefore, has the potential to significantly contribute to current interpretations of hominin evolutionary processes within an ecological framework by uncovering additional evidence for *Homo's* successful exploitation of resources under wide-ranging climate zones and ecoregions within and then beyond Africa.

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AUTHOR CONTRIBUTIONS

RP, EF, RH, and PR conceived the concepts presented throughout; all authors wrote and revised the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/feart.2021.787669/full#supplementary-material>

Supplementary Figure S1 | Stratigraphic subsections of Bed I. The expanded profile is of the FLK-N Oldowan site. Ewass Oldupa is located stratigraphically below Tuff IA and dates to 2.038 ± 0.005 Ma (Mercader et al., 2021). Stratigraphic and archeological units are not to scale except for the 3 m FLK-N profile. Dates and stratigraphy adapted from Ashley et al., 2010; Deino, 2012; Díez-Martín et al., 2015; Domínguez-Rodrigo et al., 2007; Hay, 1976; McHenry and Stanistreet, 2018; Stanistreet, 2012.

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