

Defining the ‘generalist specialist’ niche for Pleistocene *Homo sapiens*

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Definitions of our species as unique within the hominin clade have tended to focus on differences in capacities for symbolism, language, social networking, technological competence and cognitive development. More recently, however, attention has been turned towards humans’ unique ecological plasticity. Here, we critically review the growing archaeological and palaeoenvironmental datasets relating to the Middle–Late Pleistocene (300–12 thousand years ago) dispersal of our species within and beyond Africa. We argue, based on comparison with the available information for other members of the genus *Homo*, that our species developed a new ecological niche, that of the ‘generalist specialist’. Not only did it occupy and utilize a diversity of environments, but it also specialized in its adaptation to some of these environmental extremes. Understanding this ecological niche provides a framework for discussing what it means to be human and how our species became the last surviving hominin on the planet.

Debate continues as to the point at which our species emerged as a distinct hominin taxon, both morphologically and genetically, with a date around 300,000 years ago now appearing likely^{1,2}. Yet even more discussion in archaeology and anthropology revolves around the identification of unique capacities and characteristics of *Homo sapiens* that enabled it to persist beyond the extinction of other contemporaneous hominin species. Novel abilities have been sought for in the material record associated with *H. sapiens*, from 100 thousand years ago (ka) in Africa to the occupation of Europe, Asia and Sahul 60–45 ka, including evidence for symbolism, complex communication, personal ornamentation and technological sophistication^{3–6}. In turn, these material traits have been variously linked to the expression of new cognitive capacities, including specific mutations and neural architecture^{7,8}, and generally increased neural flexibility⁹. Remarkably, however, despite the fact that the colonization of the world’s continents by the end of the Pleistocene represents one of the clearest idiosyncracies of our species^{10,11}, relatively little focus has been placed on the potentially unique ecological capacities of *H. sapiens*.

Ecological characterizations of our species relative to other hominins have tended to focus on relative breadths in subsistence, sophistication of hunting practices and metabolic requirements in regions of Late Pleistocene (125–12 ka) coexistence (for example, refs^{12,13}). Alternatively, spatial modelling has been used to study differences in the geographical and environmental ranges of different hominin taxa at different points in time¹⁴. However, these studies have often been Europe-focused, missing the considerable Late Pleistocene environmental variation of the rest of the world now known to be occupied by *H. sapiens*. Where the ecological niche of *H. sapiens* in particular has been investigated, assumptions relating to ecological preferences, as well as limitations, have been used to argue for a homogeneous focus on productive ‘savannah’ or coastal routes^{15,16}, or the impassability of certain environments^{15,17,18}, during its evolution within, and expansion beyond, Africa (but see papers in ref. 19). Such approaches ignore hard, environmentally specific data accumulated over the past two decades that imply more variable ecological contexts for *H. sapiens* in the Pleistocene (for example, refs^{20–23}).

A quarter of a century ago, Gamble¹⁰ highlighted the unique ability of our species to move into ‘hard habitats’. However, he envisaged this colonization as largely occurring post-15 ka. Here, we offer a critical review of the ecological extremes inhabited by our species during the process of its dispersal across the Middle East, Central Asia, South Asia, Southeast Asia, Melanesia, Australia and the Americas during the Middle and Late Pleistocene. We focus on claims of human occupation of deserts^{24,25}, high-altitude regions²⁶, the Palaeoartic²⁷, and tropical rainforests²³, and evaluate to what extent existing palaeoenvironmental and archaeological datasets demonstrate the occupation and use of these environments by *H. sapiens* at this time. We explore the degree to which similar evidence for ecological specialization in extreme environments can be found within the Middle to Late Pleistocene record of Africa¹⁹ from which our species emerged. While these environments have often been assumed to be uninhabitable for extinct hominins and pre-Holocene *H. sapiens*, growing evidence suggests that our species is best characterized by adaptive plasticity during colonization and expansion²¹. Although, in some cases, palaeoenvironmental resolution makes quantification of the nature of such ‘extremes’ relative to those seen today difficult, we argue that the current evidence points towards a new ecological definition of our species relative to earlier or contemporaneous Pleistocene hominins.

Ecology of Early and Middle Pleistocene *Homo* dispersals

By 1.8 million years ago (Ma), there is fossil evidence for the expansion of the genus *Homo* beyond Africa and into Eurasia at Dmanisi cave, Georgia²⁸. By 1.2–0.8 Ma, *Homo* had also reached Atapuerca in Spain²⁹ as well as East Asia³⁰, and by 0.9–0.7 Ma, a hominin species had made it as far north as East Anglia in the United Kingdom³¹. It has been argued that these dispersals were linked to the climate-dependent expansion of homogeneous environments, with populations of hominins, and other African mammals, following a uniform ‘Savannastan’ into Eurasia^{32,33}. Indeed, although the Dmanisi fossils demonstrate members of the genus *Homo* had reached latitudes of 40° N, associated with no African-derived species, the forested river margins and open steppe would have presented relatively similar

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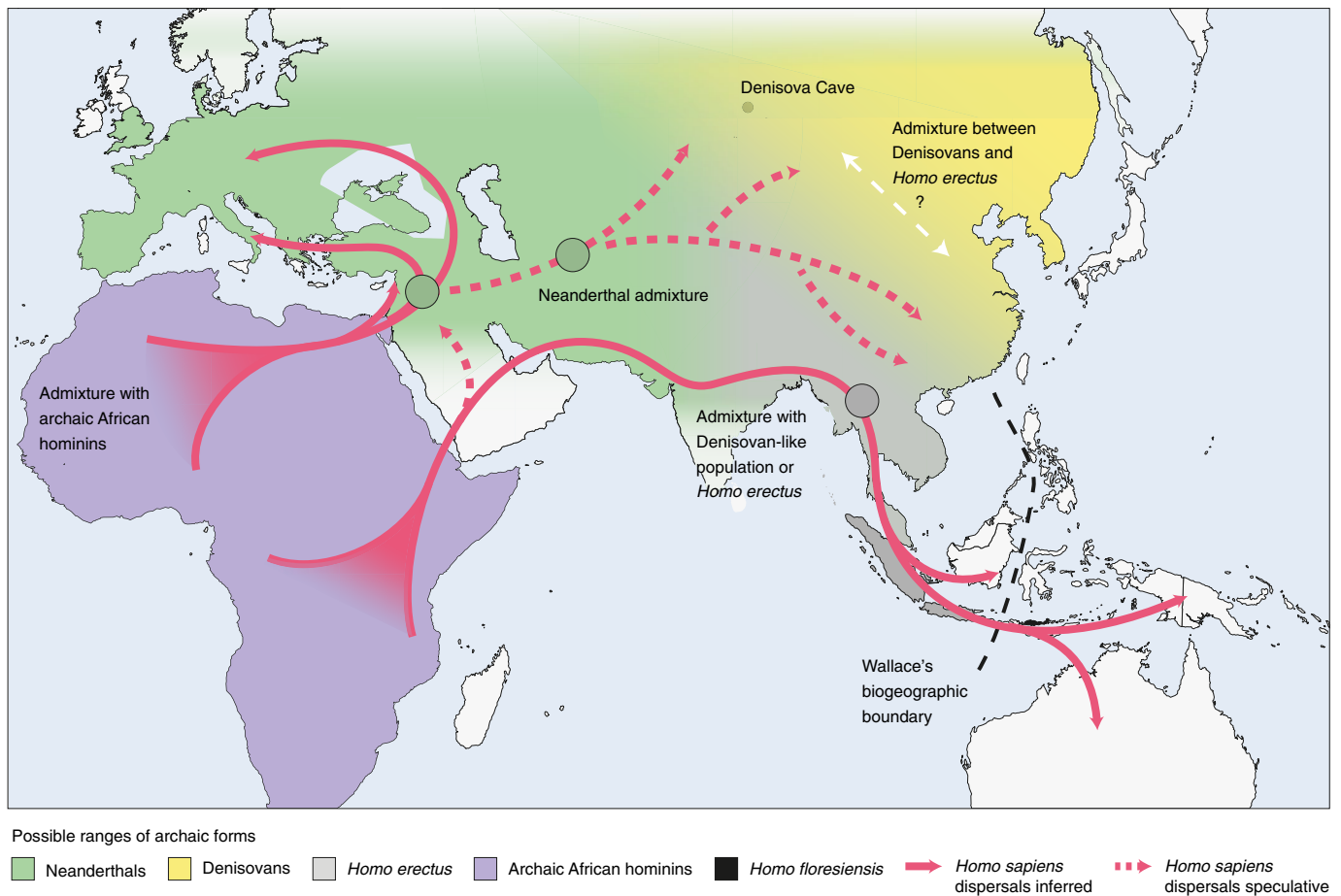


Fig. 1 | Map showing the potential distribution of archaic hominins, including *H. erectus*, *H. floresiensis*, *H. neanderthalensis*, Denisovans and archaic African hominins, in the Old World at the time of the evolution and dispersal of *H. sapiens* between ca. 300 and 60 ka (refs ^{144,145}).

adaptive choices to those faced in East Africa³⁴. Similarly, the environments at Happisburgh and Atapuerca both supported fluctuating mosaics of temperate and mesic forest, respectively, and open, dry steppe conditions^{31,35}. Comparable habitats have also been reconstructed for early *Homo* in China³⁰.

Some of the earliest Early and Middle Pleistocene *Homo* fossils beyond Africa come from the modern tropical rainforest environments of Southeast Asia (Fig. 1). Here, it has been argued that rainforest was the dominant vegetation type between 2.6 and 1.0 Ma (refs ^{36,37}), the period from which the *Homo erectus* fossils dated to ca. 1.5 Ma and ca. 1.0 Ma, in the Sangiran Formation, and Bapang and Trinil Formations, on Java, respectively, are derived^{38–40}. Similarly, small-bodied *Homo floresiensis* at Liang Bua (100–60 ka), and its putative ancestor found at Mata Menge (800 ka) on the island of Flores have been associated with physiological adaptations to insular tropical forest environments⁴¹. Nevertheless, there is no direct evidence for tropical forest use by any of these hominin taxa. In all cases, palaeoenvironmental reconstruction based on fauna or palaeobotanical studies suggests the dominance of riverine and lacustrine woodland and open grassland mosaics^{42,43}, with hominin range expansion into parts of island Southeast Asia occurring at the same time other mammals, such as *Stegodon* taxa, were moving from the mainland⁴².

In the absence of archaeological and palaeoenvironmental datasets directly linked to the Denisovan hominins, *Homo neanderthalensis* shares the greatest genetic, temporal and geographical overlap with our species^{2,44} (Fig. 1). It has been argued that Neanderthals were specialized, both in terms of subsistence and morphology, in

the occupation of relatively high latitudes, and the corresponding cold temperatures, in Eurasia ca. 250–40 ka (refs ^{45,46}). Traditionally, this has also been linked to a focus on the hunting of large Eurasian steppe game, such as the woolly mammoth⁴⁷. Nevertheless, use of a broader spectrum of animals⁴⁸, including marine resources¹² and plant foods⁴⁹, indicates dietary breadth. Moreover, palaeoenvironmental modelling has been used to argue that Neanderthals altered their ranges in the face of extreme cold and aridity^{14,50,51} and were not specifically morphologically or socially adapted to the cold⁵². Rather, the majority of palaeoenvironmental evidence links Neanderthals to varying proportions of forest and grassland habitats and the use of a diversity of mammalian game, from temperate northern Eurasia down to the Mediterranean^{49,53}. Nevertheless, it is possible that future research will expand the Neanderthal range^{54,55} and relatively few, detailed palaeoecological and palaeoenvironmental evaluations of Neanderthal habitats currently exist.

Adaptivity of Late Pleistocene *H. sapiens* beyond Africa

There is now clear evidence that our species began to expand beyond its African evolutionary cradle from ca. 200–100 ka onwards^{56,57}. Early human fossils at Herto and Omo in Ethiopia (ca. 200 ka) are associated with evidence for similar grassland and aquatic habitats to those highlighted for other members of the genus *Homo* above^{58,59}. Middle Pleistocene human dispersals into the Levant (ca. 200–120 ka) are linked to an extension of such habitats during interstadial phases of climatic amelioration^{57,59}. In the Late Pleistocene, a similar generalized focus on savannah, woodland and forest corridors, or alternatively protein-rich coastal environments, have been argued

to convey *H. sapiens* as far as Australia^{15,16,60}. Yet, rapidly accruing archaeological and palaeoenvironmental data suggest that expansions beyond Africa may have also involved often-specialized adaptations to a diversity of extreme environments little-used or wholly uninhabited by other members of the hominin clade, including deserts, high-plateau and mountain systems, the Palaeoarctic and tropical rainforests (Figs. 2 and 3).

The deserts of the Arabian Peninsula and the northwest of India had, until recently, been considered permanent, impenetrable barriers to the dispersal of hominins. However, archaeological and fossil evidence has now been used to suggest that our species made it across the central Arabian Peninsula during Marine Isotope Stage 5^{24,61,62}. It has also now been demonstrated that people carrying Middle and Late Palaeolithic technologies occupied the Thar Desert of northwestern India from 96 ka and 21 ka, respectively^{25,63}. The available palaeoenvironmental datasets from Arabia and the Thar imply that human occupation of these regions coincided with high-amplitude changes in precipitation dynamics^{63,64} that resulted in the formation of lake and river systems⁶⁵. As with earlier members of the genus *Homo*, it has been argued that human dispersals accompanied biogeographic expansions of African taxa, such as Hippopotamidae in Arabia and *Struthio camellus* in India⁶⁶. Nevertheless, potential hints at increased aridity during the Late Pleistocene⁶⁷ may complicate this picture. More refined palaeoenvironmental, and specifically palaeoaridity, data are essential to evaluate the adaptations required for the occupation of these regions by our species, as evidence for high-amplitude changes in precipitation and vegetation mean that modern conditions cannot be used as a reliable reference for adaptation. For example, palaeoenvironmental evaluation suggests that initial colonization of the central deserts of Australia at 45 ka (ref. ⁶⁸) was linked to substantially wetter conditions, with a full desert-specialist adaptation only occurring after the Last Glacial Maximum.

Specialized human adaptation to high-altitude environments has been considered a largely Holocene phenomenon^{69,70}. Yet, there is growing evidence that Late Pleistocene *H. sapiens* inhabited these settings, sometimes intensively. Particular genes in modern populations in Tibet and Nepal, that originated with non-*H. sapiens* hominins^{71,72}, have been associated with living at high elevations (>2,500 m above sea level), with evidence for selection acting on these back into the early Holocene^{73,74}. While it has been argued that these genes were essential for the first permanent occupation of the Tibetan Plateau ca. 4 ka (ref. ⁷⁵), different mutations in the past could have yielded similar results — as they have for present-day Andeans and highland Ethiopians²⁶. Indeed, although archaeological and chronological information for Pleistocene occupation of the Tibetan Plateau remains scarce, perhaps in part as a result of glacial activity, it appears that hominins using Upper Palaeolithic toolkits had colonized its peripheries as early as 30 ka (refs ^{76,77}, see also ref. ⁷⁸). Although peripheral parts of the plateau may have presented warmer, more-vegetated habitats between 40 and 25 ka, occupation would still have involved adaptation to cold, grassland expanses, and low-oxygen conditions would have prevailed throughout⁷⁸. In the Andean Plateau, dense Paleindian rockshelter deposits reported at 4,300 m above sea level in Peru ca. 13 ka (ref. ⁷⁹) not only represent the highest Pleistocene archaeological sites anywhere in the world, but remarkably also some of South America's earliest. While these may have been occupied during a humid climatic period⁷⁹, low-oxygen conditions together with cold stress and unpredictable weather would still have required novel adaptation.

A particularly definitive case for the Pleistocene occupation of extreme environments by our species comes in the form of recent archaeological evidence from the Arctic Circle (>66° N)²⁷. A mammoth kill site in the central Siberia Arctic, dated to 45 ka, indicates that humans had reached as far north as 72° N at a time of significant cold and permafrost extent²⁷. Although the

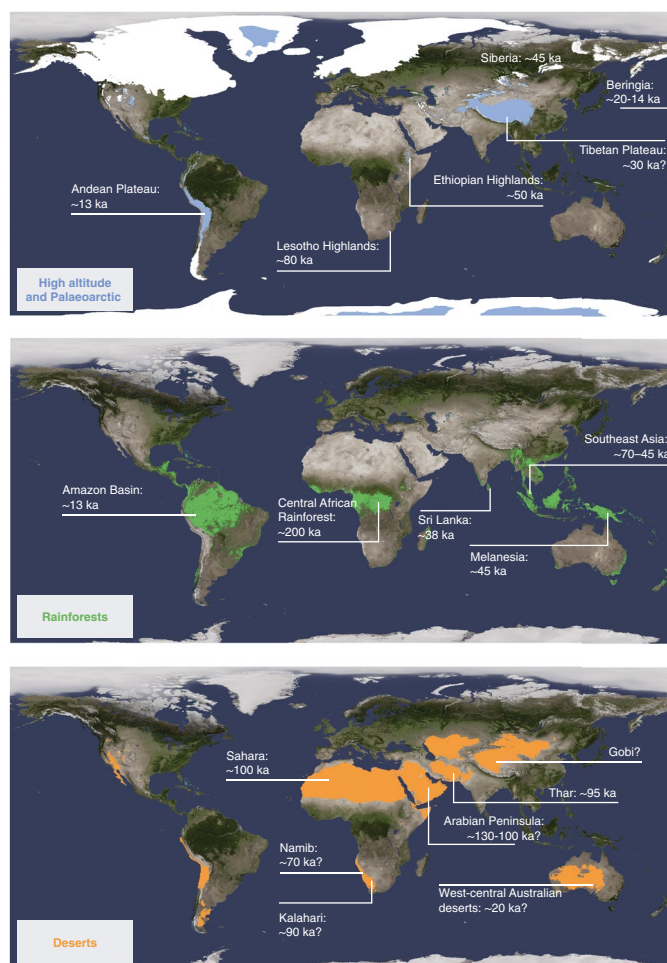


Fig. 2 | Map showing the minimum suggested dates of persistent occupation of the different environmental extremes discussed in the text by *H. sapiens* based on current evidence. High altitude classified as $\geq 2,500$ m above sea level (based on Shuttle Radar Topography Mission elevations); Palaeoarctic classified as being within the Arctic circle, with the maximum extent of glaciers documented at the Last Glacial Maximum also shown¹⁴⁶; desert classified as annual precipitation lower than 200 mm from WorldClim 2 (ref. ¹⁴⁷); and rainforest determined by the Moderate Resolution Imaging Spectroradiometer Land Cover MCD12Q1 majority land cover type 1, class 2 for 2012 (spatial resolution of 500 m). Downloaded from the US Geological Survey Earth Resources Observation System (EROS) Data Center (EDC). Credit: NASA Worldview.

northerly extent of Neanderthals cannot yet be totally discounted^{54,55}, on the balance of genetic, fossil and archaeological evidence, this currently seems most likely to have been produced by *H. sapiens*. Palaeoenvironmental research has demonstrated that extensive grasslands, akin to those found in different parts of Siberia today, would have existed in parts of Siberia even during cold periods ca. 60–40 ka (ref. ⁸⁰). However, tree-less open landscapes of cold steppe with long winters, short growing seasons, fully extended glaciers and permafrost^{80,81} (Fig. 3) still evidently necessitated a specialized hunting focus on mammoth herds that provided food as well as raw materials for tools, clothing and potentially also dwellings⁸². The production of spears from mammoth ivory also seems to have enabled the hunting of other cold-adapted fauna including woolly rhinoceros and bison in Siberia more broadly^{82,83}. Although farther south, evidence for bone-fuelled fires and mammoth bone houses in Upper Palaeolithic contexts in Western and

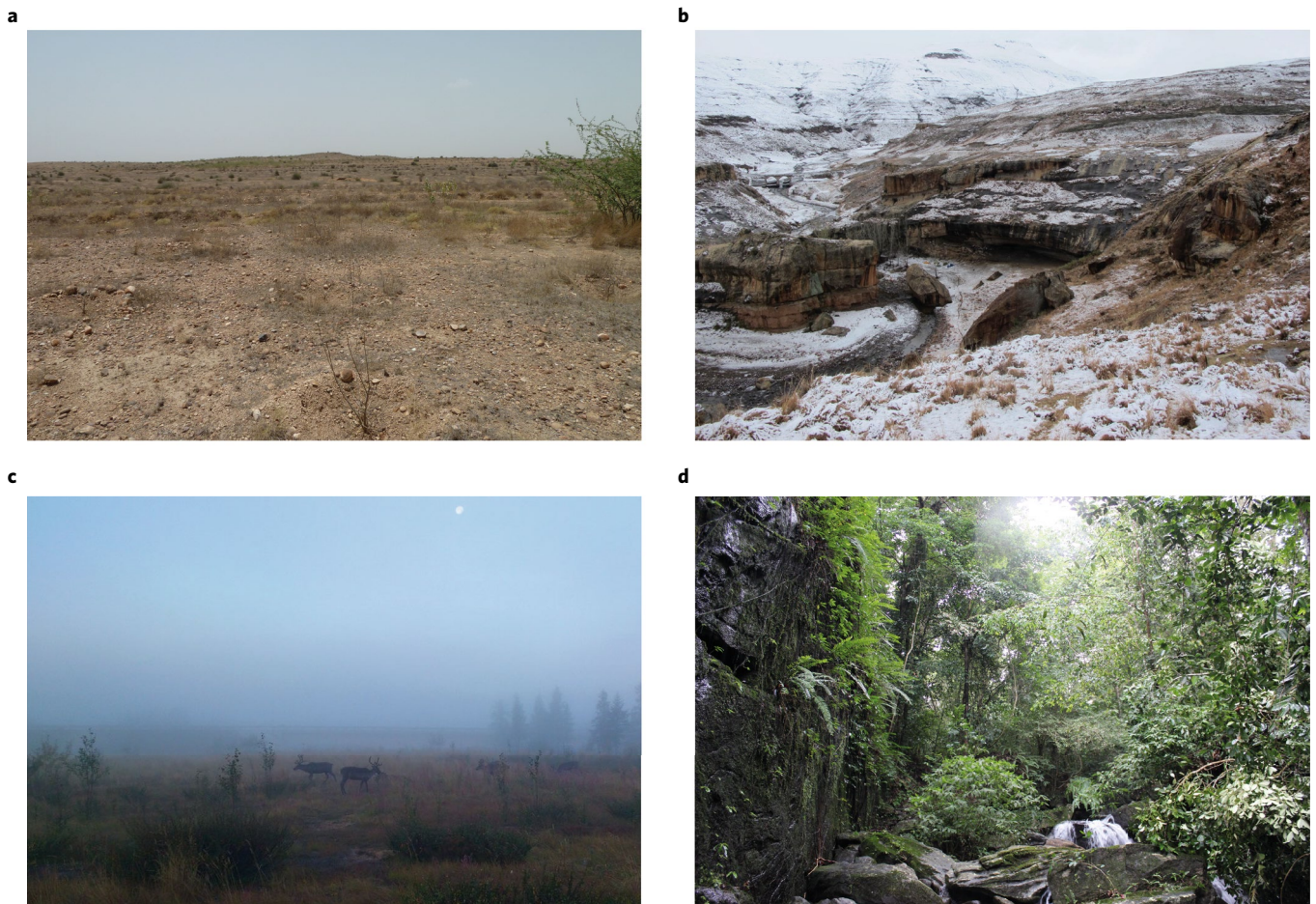


Fig. 3 | Photographic selection of some of the ecological challenges faced by Pleistocene *H. sapiens*. **a**, The Thar Desert of northwest India at the site of Katoati. James Blinkhorn. **b**, The highlands of Lesotho at the site of Sehonghong. Photograph taken by B.A.S. **c**, The Siberian steppe of Russia. Credit: Yuri Demyanov. **d**, The tropical evergreen rainforest of Sri Lanka in the vicinity of one of the earliest occupied sites in the region. Photograph taken by P.R.

Eastern Europe, respectively, suggest other further potential benefits of a mammoth hunting focus in colder climes^{84–86}.

The navigation of Arctic extremes also appears to have been aided by the maintenance of strong social networks through the manufacture of bone and ivory ornaments⁸⁷. For example, at the Siberian site of Yana Rhinoceros Horn site, decorated beads, pendants, needles, shallow dishes and anthropogenic designs on mammoth tusks are dated to ca. 30 ka (ref. ⁸⁷). Strong social relationships and a focus on large game likely also played a major role in the human navigation of the Beringia Strait into the Americas. It has often been argued that rapid occupation of the Americas in the terminal Pleistocene ca. 14 ka relied on a coastal route that avoided the Beringia Strait, or a route that relied on an ‘ice free’ corridor^{88,89}. Occupation of 72° N in Siberia 45 ka and recent new radiocarbon dates on cut-marked bone samples from Bluefish Caves, Canada dating to 24 ka (ref. ⁹⁰), however, highlights that humans may have adapted to terrestrial environments in eastern Beringia at the height of the Last Glacial Maximum. While our knowledge of the vegetation context of this part of Beringia at this time remains limited, and there may have been warmer conditions in the east relative to the west of this landmass⁹¹, occupation of higher latitudes than previously attained by any other hominin would have necessitated adaptation to cold conditions and likely necessitated similar foci on large mammals for resources for shelter, subsistence and technology. Following the occupation of Beringia, whether by coast or over land, there appears

to have been something of a delay before movement south into the rest of the Americas, however.

Clear evidence has also emerged for the Late Pleistocene human occupation and use of tropical rainforests by our species. Research over the past two decades has highlighted the manipulation of tree products, the detoxification of particular plants, and the hunting of medium- to small-sized arboreal, semi-arboreal and terrestrial tropical game in the tropical rainforests of Southeast Asia from at least 50–45 ka (refs ^{92,93}), Melanesia from 45 ka (ref. ⁹⁴) and South America from 13 ka (ref. ⁹⁵). Stable isotope evidence from human tooth enamel in Sri Lanka has highlighted that humans not only utilized the tropical rainforests of South Asia from 36–3 ka, but also occupied them and subsisted within them permanently^{96,97}. The potentially unique capacities of our species to inhabit these environments may be evident in the fact that *H. erectus* and *H. floresiensis* become extinct in Southeast Asia at a time of rainforest expansion²³. Indeed, our species also documents a series of regional specializations in its adaptation to different rainforest environments. For example, at the Niah Caves, Borneo, humans deliberately maintained a mixture of grassland, peat swamp rainforest and evergreen rainforest to exploit primates, migratory suids and a variety of plant products^{92,98}. By contrast, in Sri Lanka, dedicated monkey and semi-arboreal squirrel hunting appears to have provided adequate protein in evergreen rainforest contexts^{97,99}. The Late Pleistocene translocation of marsupials from mainland New Guinea into the Bismarck

Archipelago demonstrates a further strategy of protein provision in rainforest settings¹⁰⁰.

Unearthing the African roots of behavioural plasticity

If the ecological capacities discussed above are a uniquely human trait, we should expect to find some record of them in Africa, before or contemporaneous with dispersals beyond this continent. Unfortunately, however, efforts to answer these key questions in Africa's more ecologically extreme settings have been impeded by taphonomic complexities and geographically imbalanced research coverage. In the Sahara Desert, arguments that widespread sites with Aterian Middle Stone Age (MSA) artefacts were deposited by arid-zone specialists¹⁰¹ conflict with evidence for their frequent association with recently identified drainage basins and palaeo-lake shores indicating much wetter conditions than those found today^{102,103} (Fig. 2). Severely confounding the issue is a dearth of well-dated sites with robust palaeoenvironmental records¹⁰², and the Aterian's apparent persistence through diverse climatic phases for many tens of millennia (ca. 145–70 ka; ref. ¹⁰⁴). Similarly, notions that Central Africa's distinctive Lupemban MSA industry relates to the human colonization of dense rainforests^{105,106} (Fig. 2) have been contradicted by arguments for its association with both glacial-phase and present-day savannah environments¹⁰⁷. As Taylor¹⁰⁸ has recently shown, however, a mere 3% of Lupemban sites have been dated by methods capable of reaching beyond the radiocarbon, and only 5% have associated palaeoecological evidence. Resolution of these and similar debates must therefore await fresh empirical evidence ca. 500–100 ka.

From late Marine Isotope Stage 5, archaeological visibility and palaeoenvironmental resolution both improve. In the Kalahari Desert, for example, the earliest chronometrically dated human occupations currently range between ca. 90 and 77 ka (ref. ¹⁰⁹). Until recently, these pulses of MSA occupation were argued to loosely correlate with phases when enhanced humidity activated the Kalahari's immense inland hydrological system and associated palaeolakes (for example, refs ^{109,110}). However, a recent comprehensive sourcing study of silcrete artefacts from several of these sites, including Corner Cave, ≠Gi, Rhino Cave and White Paintings Shelter (all in Botswana), indicate that human occupations actually relate to phases of limited surface water¹¹¹. Similarly, following initial occupation of a humidified Namib Desert (85 ka)¹¹², humans appear to have developed adaptations to arid landscapes in this part of southern Africa by 70 ka at Apollo 11 Cave¹¹³ and slightly later at Spitzkloof A^{114,115}. Recent work in Africa's higher altitudes is also demonstrating phases of persistent human presence. For example, at the site of Melikane, and elsewhere in highland Lesotho, southern Africa, human populations demonstrate adaptation to relatively continental, cold and ecologically patchy environments ca. 2,000 m above sea level from at least 80 ka onwards^{22,116,117}, at times aided by a focus on equids or ample riverine resources^{116,118}.

Although the periodic partial or wholesale abandonment of highland Lesotho is likely linked to phases of extreme cold during the Last Glacial Maximum and Younger Dryas¹¹⁶, a persistent human presence through much of the Late Glacial, as well as the terminal Pleistocene and Holocene, implies significant resilience^{117,119}. Though later in time, similar arguments have been made for the site of Mochena Borago located at ca. 2,100 m above sea level in the Ethiopian Highlands. The site's small MSA faunal assemblage indicates a high-altitude, dry, open grassland environment ca. 45 ka that was similar to, or slightly drier than, today¹²⁰. Although such altitudes would not have posed health issues associated with hypoxia, their long-term occupation likely required specialized subsistence strategies and technologies to alleviate cold stress. These adaptations, as well as those associated with desert occupation, are unlikely to have evolved suddenly, and their late Last Interglacial emergence is probably more apparent than real. As with searches for

the origins of symbolism and technological complexity, there will remain inherent temporal bias in identifying the 'first' case. Yet each region does exhibit sharp contrasts between MSA and diagnostically pre-MSA archaeological site numbers beyond those explicable by taphonomic factors alone, hinting at genuine behavioural differences in the duration and intensity with which MSA tool users — presumably *H. sapiens* — exploited such environments.

The 'generalist specialist' as a new human ecological niche

The continued accumulation of more chronologically refined palaeoenvironmental datasets associated with the human crossing of the deserts of northern Africa, the Arabian Peninsula and northwest India, as well as the high elevations of Tibet and the Andes, will help to determine the extent to which novel adaptations were required by our species to enter these regions. However, on the balance of the current evidence it seems that from at least ca. 80–50 ka, *H. sapiens* expanded to higher-elevation niches than its hominin predecessors and contemporaries, and by ca. 45 ka was rapidly colonizing a range of Palaeoartic settings and tropical rainforest conditions across Asia, Melanesia and the Americas (Figs. 2 and 3). There is no cognitive or behavioural reason why other members of the genus *Homo* could not have utilized diverse environments, and varying degrees of technological complexity, symbolic behaviour and social networks have been documented for *H. neanderthalensis* and *H. erectus*^{121–123}. Furthermore, non-*H. sapiens* Pliocene and Pleistocene hominins undoubtedly adapted to significant climatic and environmental variability across much of the Old World^{14,30,124,125}. Nevertheless, while new high-latitude, temperate and tropical habitats were certainly encountered and perhaps even sporadically used by non-*H. sapiens* hominins both within and beyond Africa, their primary ecological niche consistently appears to have been a generalized utilization of different forest and grassland mosaics proximate to riverine and lacustrine settings^{10,11}.

While *H. sapiens* continued the use of diverse grassland, temperate forest and coastal environments, from at least the Late Pleistocene, it also apparently began to inhabit a huge diversity of other settings across the majority of the Earth's continents. We propose that this is indicative of a novel niche for our species, that of the 'generalist specialist'. The traditional ecological dichotomy between 'generalists', who can make use of a variety of different resources and inhabit a variety of environmental conditions, and 'specialists', who have a limited diet and narrow environmental tolerance, has already proven inadequate in the face of evidence for individual dietary 'specialists' existing among a 'generalist' population^{126–129} (Fig. 4). While a population may incorporate resources from multiple food webs, individuals may subsist on a discrete food web¹²⁹. However, we argue here that the Middle and Late Pleistocene record indicates that intrapopulation specialization occurs in *H. sapiens* at the level of an entire local population, rather than individual. Our species demonstrates the utilization of a diversity of environments and a broad ecological niche (Fig. 4). Yet, it also demonstrates the ability to simultaneously specialize its subsistence within these individual environments for millennia, including the coasts of South Africa¹³⁰, the high elevations of eastern and southern Africa, the tropical rainforests of Asia and beyond, and the Palaeoartic. Moreover, *H. sapiens* is able to specialize at still finer scales, for example, in tuning subsistence to montane versus evergreen rainforest^{95,131,132}.

The ecological literature also provides hints as to how such a niche may have been maintained. 'Individual specialization' within a population has been argued to be driven by a variety of potential factors including (1) resource scarcity, (2) inter-habitat differences in resource availability, (3) fitness trade-offs resulting in individual-specific behaviour and (4) cultural transmission of foraging traditions¹²⁹. Here, the fourth factor listed may provide a useful link between existing hypotheses of cumulative culture and extensive non-kin cooperation in Pleistocene *H. sapiens*¹³³, and the

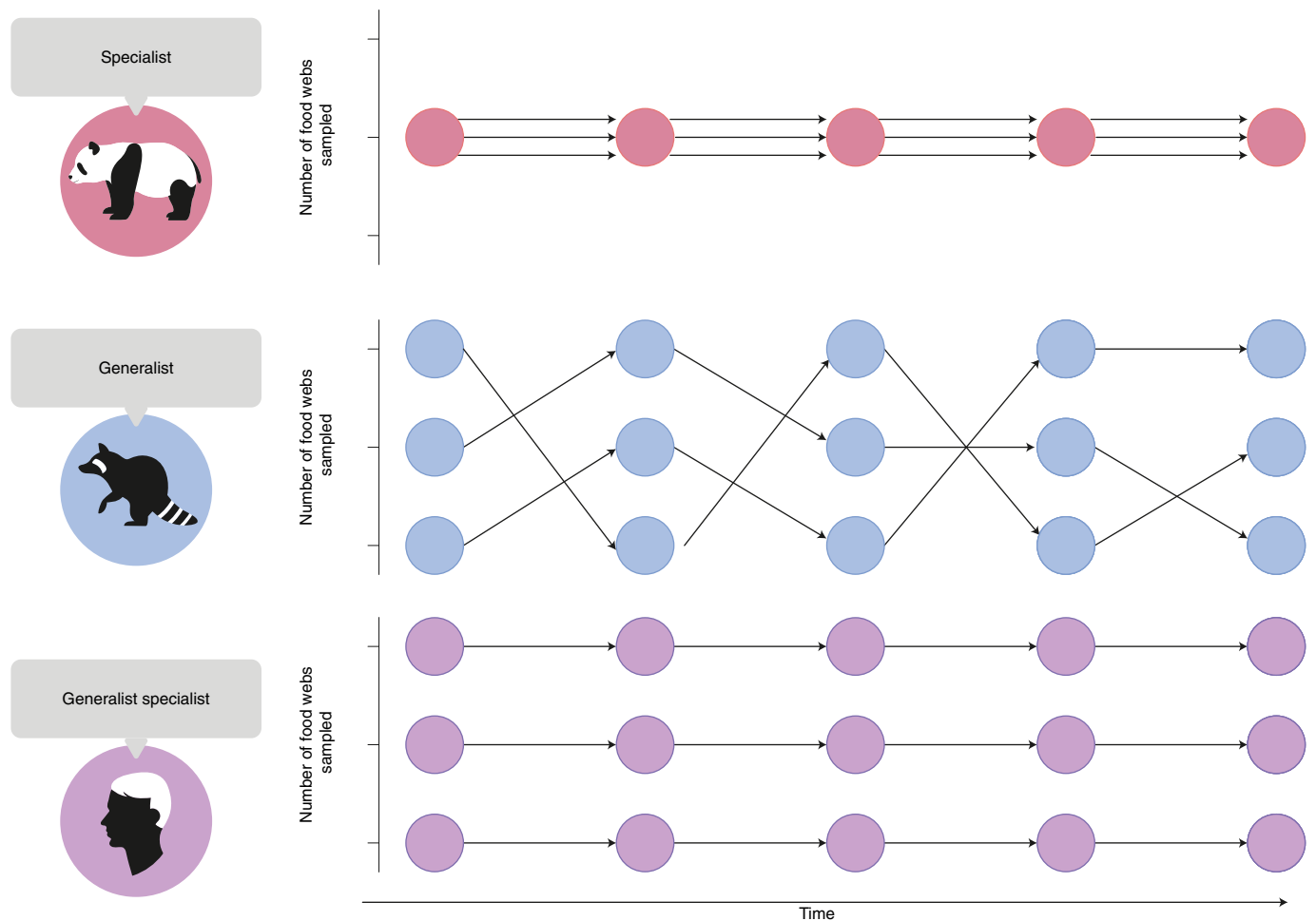


Fig. 4 | Schematic of the utilization of different numbers of food webs by generalist and specialist populations, and the proposed unique human niche of ‘generalist specialist’¹²⁷. Local populations of a specialist species will all maintain a specialist use of a single food web through time. Local populations of generalist species will utilize a variety of different food webs through time. While *H. sapiens* are often highlighted as a classic example of a generalist species in this regard, local populations of our species are also able to specialize in the use of different food webs through time; hence, the generalist specialist.

maintenance of a generalist specialist niche. In these models, it has been suggested that non-kin food sharing, cooperative food acquisition exchange and ritual relationships¹³⁴ allowed populations to ‘reflexively’ adapt to local climatic and environmental fluctuations, and outcompete and replace other hominin species¹³⁴, by changing cultural, and even demographic, parameters^{135,136}. Ecological, biological and cultural evolution is seen as intersecting at the level of local population, whereby “none of us is nearly smart enough to acquire all of the information necessary to survive in a single habitat” but we have a “uniquely developed ability to learn from others” (p. 10918 in ref. ¹³⁵). We suggest that this capacity for accruing, drawing from and passing down a large pool of cumulative cultural knowledge, material and intangible, may have been crucial in the creation and maintenance of the generalist specialist niche by our species in the Pleistocene.

The ability to simultaneously generalize and specialize would have had competitive implications in the face of increased environmental variability that framed the evolution and expansion of our species^{20,21}. Other hominins were also able to expand across the planet, and be resilient in the face of climate and habitat change through movement and range contraction. However, the prevailing evidence suggests that as their favoured grassland, woodland and forest mosaics contracted with increasing cold and aridity in Eurasia from ca. 40 ka (ref. ¹³⁷), and with the expansion of rainforest

in Southeast Asia from ca. 80 ka (refs ^{23,42}), they were likely at a disadvantage relative to *H. sapiens* entering those regions. While these hominins adapted to climatic and habitat change through mobility and range contraction, reliance on grassland and woodland resources, in the broadest sense, may have left them ecologically and demographically fragile as their mosaic corridors of movement and connection were lost due to extreme changes in sea-level, rainforest, glacier or desert expansion, or increasingly cold temperatures at high altitude. Although this apparent ecological contrast with our own species may be a result of taphonomy, as well as deliberate choices made by other hominin populations in the habitation of open-air lakeshore sites with poor preservation, where well-preserved cave and rock-shelter deposits are associated with *H. neanderthalensis* and *H. floresiensis*, there is no evidence for specialized adaptations (see refs ^{23,50,51}). By contrast, the stability of the adaptations of local populations of *H. sapiens* to diverse, and dynamic, environments can be seen across the Late Pleistocene into the Holocene.

This hypothesis urges a new focus on archaeological survey in more extreme environments, including those, such as the Gobi Desert¹³⁸ and Amazon rainforest formations¹³⁹, that are not covered here in detail, as well as the hope of detailed archaeological and palaeoenvironmental sequences in settings such as the western and central African rainforests^{106,108,140}. Furthermore, while new fossil and genetic discoveries are revealing hitherto unknown taxonomic,

biological and demographic insights, the growing evidence for mosaic features, geographic structuring and variable interbreeding, within and beyond Africa, emphasizes the importance of enriching our ecological understandings of different hominin taxa^{1,103,141}. We need more refined palaeoenvironmental and palaeoecological datasets, including faunal analysis, archaeobotany and stable isotope research (among others), that can be reliably associated with different hominin taxa. Moreover, we require enough resolution to determine the necessity of ecological specialization between these taxa, and to be able to determine environmental parameters in the past relative to the present. For example, a focus on ecological definitions of our species goes hand in hand with use of ancient DNA not just for taxonomy and demography, but also to study environment-based selection for certain characteristics in hominins^{142,143}.

In addition, if *H. sapiens* truly is a generalist specialist, this has significant implications for how we model it as an agent when testing the interrelation of climate, environment and demography during Pleistocene dispersals (for example, ref. 18). Indeed, given the potential role of cumulative culture and cultural niche construction in this process, it is important to stop viewing the archaeological record as a passive reflection of certain cognitive capacities or environmental responses⁹. Instead, if the origins of our species lie in a process of ecological and cultural coevolution, we must understand how changes in subsistence, changes in technology, changes in cultural communication and changes in palaeodemography may have persistently interacted with the local, dynamic environment to produce new local specialist populations across space and time. While, as with other definitions of human origins, taphonomic issues also make it difficult to pinpoint the origins of such behaviours⁵, an ecological perspective on the origins and nature of our species potentially illuminates the unique path of *H. sapiens*, relative to other hominin ‘timewalkers’¹⁰, as it rapidly came to dominate the Earth’s diverse continents and environments. The ability to adapt to extreme environments, inherent in global colonization, is clearly not limited to the Last Glacial period¹⁰, however, and we have demonstrated the possibility that such capacity likely defined *H. sapiens* since its first emergence in Africa. The testing of this hypothesis should open up new avenues for research and, if correct, new perspectives as to whether the generalist specialist will continue to be an adaptive success into the future.

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Author contributions

P.R. and B.A.S. designed this manuscript, analysed and interpreted the data, wrote the manuscript, and revised the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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