旧石器时代古人类和智人在东亚的扩散

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摘 要：扩 散 (dispersals)、殖 民 (colonisation)、移 入 (immigration)、人 口 同 化 (assimilation) 或 取 代 (replacement) 是东亚旧石器考古的基本主题。其中的一些主题，可以在生物地理学的框架内进行研究，主要通过研究古人类对气候和环境变化的响应，来阐释古人类种属在空间和时间上的变化及背后的原因。古人类 (hominins)[尤其是智人 (humans)] 的行为受到技术、社会和认知发展等因素的影响，因此，在研究扩散时，生物地理学模型也必须包含对这些因素的思考。对于智人在东亚扩散至雨林，跨越海洋到达离岸岛屿，甚至到达北极和青藏高原最高地区的研究来说，这些因素尤为重要。以上述思考为基础，本文提出了一个研究古人类和智人在东亚扩散的方法论框架，该框架以生物地理学框架为基础，同时结合了古人类适应性和行为变化的因素。

关键词：古人类；智人；扩散；东亚；生物地理学

Hominin and human dispersals in palaeolithic East Asia

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Abstract: Dispersals, colonisation, immigration and population assimilation or replacement are fundamental themes in the Palaeolithic record of East Asia. Some of these issues can be studied within a biogeographic framework that explains why and how the distribution of hominin species changed over time and space in response to climatic and environmental change. Because hominins (and especially humans) can change their behaviour through technical, social and cognitive developments, biogeographic models also have to incorporate this factor when investigating dispersals. This is particularly important with the dispersals in East Asia by Homo sapiens into rainforests, across open sea to off-shore islands, to the Arctic and the highest parts of the Tibetan Plateau. This paper suggests how hominin and human dispersals in East Asia might be investigated by using a biogeographic framework that can incorporate changes in hominin adaptability and behaviour.

Keywords: Hominin; human; dispersal; East Asia; biogeographic

1 Introduction

Investigations of human evolution within a biogeographical framework began very early in East Asia [1)][1]. The German zoologist Ernst Haeckel (1834-1919) proposed in 1868 that apes and humans originated on a lost continent called Lemuria, which sank in the Indian Ocean: the ancestors of chimpanzees and gorilla were then supposedly washed ashore in Africa and the ancestors of humans and orangutans reached SE Asia, from which hominins evolved into humans and eventually dispersed worldwide. Although his scenario lacked any supporting evidence, it encouraged Eugene Dubois to seek employment as a doctor in the Dutch East Indies. Haeckel's theory seemed confirmed in 1891 when Dubois found at Trinil, Java, the skull and femur that he named Pithecanthropus, a term that Haeckel had proposed as the first human ancestor. In the early 20th century, Henry Osborne (1857-1935)[2, 3] proposed that human origins lay in Central Asia (defined as Mongolia, Tibet and Inner Mongolia). His ideas were expanded by the American researcher William Diller Matthew (1871–1930), whose paper "Climate and Evolution" was published in 1915[4]. In his model, the uplift of the Tibetan Plateau blocked the summer monsoon and caused the drying out of Central Asia (defined primarily as Inner Mongolia and Xinjiang in China, and Mongolia). As a result, the species inhabiting Central Asia would perish, adapt to drier conditions, or leave. However, the uplift of the Himalayas created a barrier that prevented species from moving to the forests of South and Southeast Asia. He further proposed that those species in the center of the "cradle" were dynamic and adaptable, but those on the edges were conservative and passive, and simply moved to familiar environments elsewhere. They were then displaced even further by the more dynamic species in the center that had adapted to new, more arid conditions and were able to radiate outwards and colonize new environments. As part of that narrative, these primitive types included the ancestors of gorillas and chimps that were displaced to Africa by the more dynamic hominins[5]. In Matthew's view, "The most advanced stages should be nearest the centre of dispersal, the most conservative stages furthest from it"[6]. He effectively inverted Darwin's suggestion that humans evolved in Africa because that was where our closest cousins are found; for Matthew, the existence of the chimpanzee and gorilla in Africa indicated that they had been dispersed there by more advanced types (such as humans) that originated in Central Asia. These ideas were developed by the Canadian Davidson Black (1884-1934), who sought employment at Peking Medical College in order to be near this potential centre of human evolution. His papers[6, 7] (and further discoveries at Chou-kou-tien and localities such as the Nihewan Basin and

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1) I define East Asia as comprising China, Mongolia, Russia east of Novosibirsk and the Altai Mountains, mainland Southeast Asia, Indonesia (which includes the Sunda Shelf and the islands of Wallacea), the Japanese islands and the Philippines.

Shuidonggou by Licent and Chardin in 1922[8, 9]) did much to establish Central Asia as the most likely cradle of humankind. Just as Dubois discovered a human ancestor at Trinil, so Black was instrumental in recognising Sinanthropus as a human ancestor in 1927 on the basis of one tooth from Chou-kou-tien. It was only after WW2 that Australopithecus was recognised as a hominin and Africa was accepted as a more likely place where hominins originated[10, 11].

Although the ideas of Haeckel, Matthew, Black and others about the primacy of East Asia in human origins are now historical curiosities, they are rare examples where theories about human evolution were in place before discoveries appeared to confirm them. A century after the Swedish geologist Andersson made the first discoveries at Chou-kou-tien, it is appropriate to suggest how biogeography can contribute to our understanding of the deep past of humanity in East Asia.

An enormous amount has been learnt in the last 20 years about the palaeolithic, Pleistocene and human skeletal record of East Asia. As highlights, we can note that there are now good faunal records from the Arctic, Siberia, China, the Japanese islands and SE Asia; a superlative climatic record from the loess-palaeosol sequence of the Loess Plateau, supplemented by the loess-palaeosol record of Central Asia and marine cores from the south China Sea; and three new hominin species (Denisovans, *H. flore-siensis* and *H. luzonenensis*) have been discovered in East Asia in the last 20 years[12, 13]. All this new information opens up opportunities for more ambitious objectives than writing culture sequences. Here, I propose that a biogeographic perspective could help illuminate the complex and rich record of hominin (including human) dispersals in Pleistocene East Asia. Central concerns of biogeography are to explain the present-day distribution of species, their origins and how and why their distribution changed in the past. Palaeoanthropology has much the same agenda, but one that is complicated by the need to explain how and when our own species became the only hominin on the planet.

*Hominin dispersals and biogeography in East Asia*

One reason why East Asia is such an exciting region for studying Pleistocene hominins is that it is unique in encompassing two biogeographic Realms – the Oriental Realm of South China and SE Asia (with a sub-realm of Wallacea) and the Palearctic Realm of North China, Mongolia, Siberia (with its own sub-Realm of the Arctic), and the Japanese Islands, with the Qinling Mountains forming the boundary between the two in China (Fig. 1). (For those unfamiliar with the term, a biological Realm is an area of the earth's surface that contains fauna and flora that share the same evolutionary history [2]). Hominins in the Palearctic Realm were usually dependent on seasonal plant foods and a small number of herbivores as prey that were often migratory, and sometimes over large distances (such as horse, reindeer and gazelle). Hunter-foragers in the Palaearctic Realm often faced considerable risk in their dependence on a small range of food resources, and considerable uncertainty over their predictability[14]. The Oriental Realm contained a far larger range of plant resources, had a more equitable climate, but fewer herd animals than

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2)　Biological Realms were first proposed by biogeographers Philip Sclater and Alfred Wallace in the 19th century. Since then, there have been numerous attempts to refine or redefine their schemes, but for the purposes of hominin biogeography in East Asia, their recognition of a Palearctic and Oriental Realm are still useful.

the Palearctic Realm, and there was less likelihood that a region would become uninhabitable during a climatic downturn. Because diets were more broadly based in the Oriental Realm, there was probably less risk of starvation if a key resource failed and a larger range of fall-back options. Consequently, hominin occupation in these two realms followed very different paths; populations in each realm often developed in isolation from the other, but at other times, they interacted. Additionally, the boundaries of the Palearctic and Oriental Realms in China shifted when the climate changed[15], so some animals such as panda (Ailuripoda) occasionally and Hystrix, Macaca and others frequently expanded their distribution north of the Qinling Mountains in warm periods, although only a few Palearctic species extended south of these mountains during cold ones[16].

There are several ways in which biogeography is a useful way of studying dispersals of Pleistocene hominins in these Realms. Its main advantage is that it places hominins within a climatic and environmental context that allows different types of evidence (skeletal, archaeological, faunal, botanical etc.) to be studied in an integrated manner. A biogeographic approach is also appropriate for studying hominins at a continental or regional level and over long time-spans of the Pleistocene. A third advantage is that it is a useful way of examining the opportunities and challenges faced by hominins when adapting to the different types of environments in the Palearctic or Oriental Realms.

When dealing with hominins, two additional factors need considering. The first is that
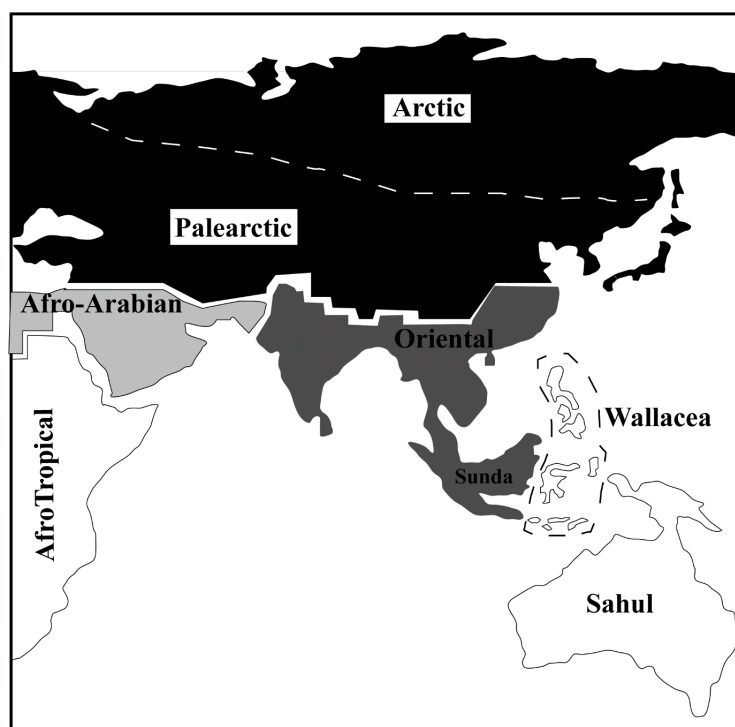
Fig. 1 Biogeographic realms and sub-realms of Asia. The two sub-realms are the Arctic (as a sub-realm of the Palearctic) and Wallacea (as a sub-Realm of the Oriental Realm)

Sea-levels are shown at 40-60 m below present levels for the Arabian-Persian Gulf, Sunda and Sahul. Redrawn and modified from [17] Fig. 1.

hominins (including humans) are unmatched in their capacity for adaptive change through developments in technology, social organisation and cognitive ability. Whereas biogeographic studies of rabbits or rhinos, for example, can assume that their behaviour has not changed substantially in the last two million years, studies of hominins always have to incorporate their capacity for adaptive change in behaviour. A second factor that greatly complicates the study of hominin biogeography in East Asia is that it was occupied by several types of hominins for most of the Pleistocene until replaced by Homo sapiens. In regions of East Asia already occupied by indigenous hominin populations, immigration, and population assimilation and/or replacement by *H. sapiens* are major themes when considering how humans became the sole hominin resident.

2 Biogeographic modelling of hominin dispersals in East Asia

Two sets of models can be used to explain past dispersals of hominins. The first are those where the driving force is the environment – climatic and environmental change, or the behaviour of the fauna. The second set is unique to hominins, and are changes brought about by their adaptive responses that led to changes in behaviour which in turn opened up new opportunities for dispersal and colonisation.

2.1 Preliminary considerations

First, some points about terminology. A dispersal is the same as range extension – the process by which a species extends its distribution into areas previously unoccupied. Range extension always occurs at the edge of an animal's range and therefore usually involves directly only a small portion of the total population. Migration in bird and animal populations refers primarily to seasonal movements between winter and summer territories; for example, migrating populations of deer or geese will make a two-way journey to and from a winter or summer feeding ground. Social scientists often use the terms "migration" and "dispersal" as though they are interchangeable. This leads to confusion, and the term "migration" should be restricted to discussions of seasonal, two-way movements. In modern human populations, migration is often used to mean people moving from one country or region to another without making a return journey: with internal migration, from village to city inside a country, or with external migration, from Mexico to the United States, for example. Hence, we talk about immigration and emigration, although these should be more accurately be referred to as dispersals. Here, I confine "migration" to meaning seasonal movements, and dispersals as implying an extension of an animal's range.

Metapopulations and palaeodemes

Human populations, like those of many other mammals, are structured in that the total population is composed of numerous sub-sets that are called metapopulations[18] (Fig. 2). These are spatially separated and inter-dependent parts of networks that share information, mating partners and sometimes scarce materials. Humans are extremely good at forming tight metapopulations that are

large, complex, mutually supporting, and have a high degree of connectivity between them. In studies of later prehistory, these networks have attracted much attention, and there are obvious connections between studies of archaeological networks and demographic metapopulations. In the Late Pleistocene, these tight metapopulations were crucial factors in the colonisation of new areas such as the Arctic, rainforests, Australia, Wallacea, the Japanese islands and the Americas. An unfortunate reality about Palaeolithic evidence is that it is exceptionally difficult to identify specific archaeological networks of metapopulations from lithic and (sometimes) bone, antler or artistic evidence.

Palaeodemes in human evolutionary studies are the equivalent of metapopulations. Howell[19, 20] stressed the importance of the palaeodeme as "the basic stuff of the hominin fossil record"[19] as a unit of analysis in palaeoanthropology. A deme is "a communal interbreeding population within a species …… distinguishable by reproductive (genetic), geographic, and ecological (habitat) parameters." Together, demes (sometimes as isolated populations) constitute subspecies, or the "aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species"[19]. China is one of the few regions of Asia where it is possible to demonstrate local palaeodemes from its detailed skeletal record[21].

2.2 Models of dispersal driven by environmental factors

We can begin by considering simple biogeographic models that are driven by changes in climate and environment and which are applicable to all periods of the Pleistocene. Some of these are appropriate for studying north-south dispersals, and others for ones that run west to east. The relevant background evidence is summarised in Dennell[12, 13].
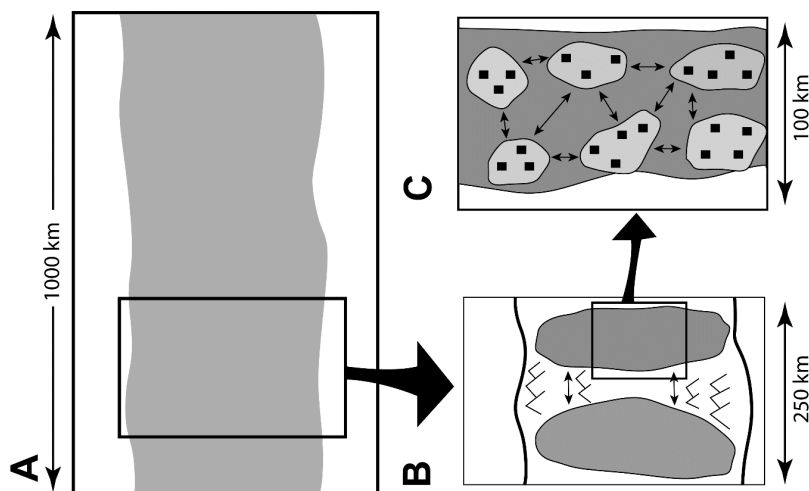
Fig. 2 range and metapopulation distribution

Within the total range of a species (A), there would have been spatially separated but inter-dependent populations (B). At a smaller scale, each metapopulation would have comprised further sub-sets of subsistence groups (C) whose membership was largely constant from year to year, and whose monthly and annual movements were usually over the same territory. These groups would form networks within which mates, resources, and information could be exchanged. The distances shown in these figures is intended only to show relative differences in the scale of analysis.

Ebb and flow models

At a species level, an ebb and flow model is the simplest way of modelling the north-south dispersal of hominins within continental Asia in response to changes in climate. For those unfamiliar with the sea or those for whom English is not the native language, ebb and flow refers to the twice-daily fall and rise of the tide. The image of tidal range provides an appropriate way of envisaging the likely north and south movements of hominins in continental East Asia in response to climate change.

In Europe and North America, the main factor determining the distribution of plants and animals was the repeated advances and retreats of ice sheets that marked glacial and interglacial/interstadial periods. As ice sheets and glaciers expanded in glacial periods, cold-intolerant species (such as hominins) retreated south into glacial refugia, and cold-tolerant species (such as Arctic lemmings and musk oxen) expanded south from their interglacial refugia. When ice sheets contracted in warm periods, hominins and other cold-intolerant species could expand out of their refugia and recolonise areas previously abandoned, and cold-tolerant species retreated northwards into their Arctic biome. Consequently, the record of hominin occupation in Asia in the Early and Middle Pleistocene is predominantly a record of occupation in warm periods and abandonment in cold ones[22, 23].

In East Asia, ice-sheets were far less significant than in northwest Europe and North America, so the contrast between cold and warm periods is not defined by the limits of ice sheets. Instead, the main contrasts in East Asia are mean annual temperature (MAT) and mean annual precipitation (MAP) that are determined by the relative strengths of the winter and summer monsoons. In cold, dry periods, the winter monsoon pushes cold, dry air from Siberia and Mongolia further south than in warm, moist periods, when the summer monsoon is able to deliver rain from the Pacific and Indian Oceans further north than in cold, dry periods. These shifts in rainfall determine the boundary between the arid and semi-arid regions of China and Central Asia, and that in turn affects the distribution of hominins.

One area that shows a pattern of repeated hominin expansion and contraction in response to climate change is the Chinese Loess Plateau, with its superlative sequence of 32 major loess and palaeosol units denoting cold and warm periods. Today, mean annual temperature at Xifeng in the Central Loess Plateau is 8.3 °C and mean annual precipitation is 560 mm. At its extremes, during the formation of palaeosol S4 (360-412 ka), S5-1 (479-531 ka) and S5-3 (585-621 ka), the Loess Plateau was sub-tropical and semi-humid, with 200-300 mm more rain than at present and 4-6 °C degrees warmer[24]; when loess L9 (865-943 ka) and L15 (1.24-1.26 Ma) were deposited, it was like a polar desert with an annual average temperature of only 1.3 – 3.0 °C degrees and only 150-250 mm of rain[25]. During very warm and humid periods, panda browsed in the southern parts of the Loess Plateau[26], whereas during the LGM, woolly mammoth grazed as far south as the Qinling Mountains[27]. One would thus predict that the Early and Middle Pleistocene hominin occupation of the Loess Plateau was largely confined to warm periods. Field data conforms this. For example, fieldwork in Lantian county in the southern Loess Plateau shows that hominins were present in 17 warm periods but only 4 cold ones between 2.1 and 1.2 Ma-ago[28]. In cold periods, the Plateau was

largely abandoned in favour of refugia in valley basins in the Qinling Mountains such as the Luonan and Lushi, where ca. 270 palaeolithic sites that date from 1.2 Ma to the last glacial cycle have been found[29, 31]. These basins were occupied in cold as well as warm periods. The Yangtse Valley was also another likely glacial refugia for southern populations no longer able to inhabit northern China[32].

The deserts of North and Northwest China – the Northern Arid Area of China (NAAC) – is another area where we would expect hominins to be present only during periods when rainfall was higher. The Nihewan Basin, which lies north of the Loess Plateau but south of the NAAC, is another area that I have argued was occupied predominantly in the summer months of warm periods during the Early and Middle Pleistocene[33], and not continuously as suggested by some researchers[34, 35].

There is also an altitudinal element in this type of climate-induced dispersal: as snow lines retreated in warm periods, highland areas became inhabitable for warm-loving species, and cold-tolerant ones had to retreat to higher elevations. We might thus expect the hominin occupation record in high-elevation regions such as the Tibetan Plateau and Himalayas to be limited to warmer periods when snowlines retreated. The site of Nwya Devu at 30-45 ka and 4,600 m asl[36,37] may be one example of short-term occupation of the Tibetan Plateau by *H. sapiens* during a warm part of the last glacial cycle. The Xiahe mandible from Baishiya Karst cave at 3,280 m asl is more problematic. Three U-series samples of carbonate from the base of the mandible produced dates of c. 160 ka, which is in the middle part of the cold period MIS 6. It seems improbable (at least to the author) that hominins were able to cope with both high elevations and low temperatures, as severe as in MIS 4 and MIS2, as early as 160 ka-ago. We need to understand better the length of the interval between the death of the Xiahe individual and the formation of the carbonate crust. Additional dating might also confirm the current dating of 160 ka.

One major strength of ebb and flow models is that they are testable in two ways. The first is to place sites in a climatic context, as in the Chinese Loess Plateau. Secondly, it may be possible to obtain data on seasonality from faunal data, and estimates of temperature from proxy indicators such as insects[38] or soil chemistry[39].

Although a simple ebb and flow model is useful in modelling the dispersal of hominins across continental Asia and their movements northwards during warm, moist periods, it has three main limitations. The first is the assumption that when conditions worsen, populations retreated back into their refugia. This unlikely because when conditions worsened, all populations would have been under stress, including those in refugia. Instead of populations retreating into refugia, it is more likely that there was a high rate of group extinction, particularly at the edge of the hominin range[40]. This might have been occasionally catastrophic – for example, entire groups might perish in a blizzard or during an exceptionally cold winter – but was probably attritional in most cases. Small groups are highly vulnerable to extinction through random fatalities caused by accident or illness, by the small number of females that can bear children, by their rates of survival, and by inevitable fluctuations in food supply. Consequently, population levels are likely to have fallen sharply during climatic downturns. Tallavaara et al. estimate that in Europe, populations totals decreased from

ca. 410,000 to 130,000 between 30 ka and 13 ka[41]. In a first attempt to model population levels in China over the last 50 ka, Wang et al. plotted radiocarbon dates from archaeological sites in different regions of China against the climatic record and inferred that population size was linked to climate[42] (i.e., the number of dates per period was an approximation of relative population size). Unsurprisingly, they suggested that population levels fell sharply during cold, dry periods of the last glacial cycle. (They also emphasized that their conclusions needed testing with archaeological and environmental data). The second weakness of an ebb and flow model is that it treats hominins as totally passive when experiencing climatic and environmental change. Whilst it may be appropriate to model the behaviour of Early Pleistocene hominins in the same way as mice or mammoths, it is much less appropriate when discussing later hominins, who often used cultural adaptations that enabled them to colonise regions that earlier hominins could not. As seen later, these adaptations had profound consequences in East Asia. The third limitation of an ebb-and-flow model is that it is unable to explain complexity and variability in hominin skeletal and archaeological records. Here, a source-sink model is more effective (see below).

Habitat fragmentation, loss and recombination: barriers and corridors

Ebb and flow models can be effective ways of modelling hominin movements from north to south, but are less useful in explaining dispersals from east to west. One approach that may be useful is to consider how climate change creates barriers or corridors by habitat loss, fragmentation, or recombination. The most extreme example of habitat loss in Pleistocene East Asia is the drowning of the Sunda Shelf during interglacials that halved the area of land and created numerous islands. In continental East Asia, areas of deserts might become semi-arid grassland during a warm, moist period, and the increased extent of grassland along desert margins might open an east-west corridor for dispersal by hominins and other animals[43]. Li Feng et al.[44] have suggested that ca. 35-45 ka-ago, one such corridor open up that allowed *H. sapiens* to enter North China via the margins of the Taklamakan desert instead of from Transbaikalia and Mongolia. In this scenario, humans would have relied upon the streams fed by meltwater that flowed from the Kunlun Mountains to the south or the Tienshan to the north. This suggestion needs testing by fieldwork, but there are various indications that the Taklamakan was at times more conducive to human settlement than now: Weiwen et al.[45] reported stone artefacts on the southern edge of the Tarim Basin; a grinding stone with starch grains of grasses and dated at 13 ka has been found in the hyper-arid Lop Nor Basin[46]; Han et al.[47] report a hearth and stone artefacts dated to ca. 7,000-7,600 ka from the hyper-arid Tarim Basin.

As another example, areas of dense sub-tropical forest in South China or SE Asia might have fragmented under cooler and drier conditions, and the resulting mosaic landscape of dense forest, open woodland and perhaps some grassland would have created favourable conditions for hominins and also open corridors for dispersal[48]. Conversely, all these corridors could become barriers during periods of climatic change. It is important to note that habitat fragmentation that benefitted

hominins could occur in both cold, dry periods and warm, moist ones: cold, dry periods would have increased the extent of desert in Central Asia but created a mosaic landscape in SE Asia, and warm, moist periods benefitted hominins in areas where deserts retreated, but not necessarily those in areas that became dense sub-tropical and tropical forest or were threatened by rising sea levels.

On a very large scale, ebb and flow models are useful in showing that range expansion northwards in central and east Asia became increasingly difficult in the Middle Pleistocene because the expansion of deserts converted much of what I previously called "Savannahstan" into "Aridistan"[12, 43, 49], and thereby created barriers against dispersal either north-south or west-east. In China, the southern margin of the Mu Us Desert advanced southwards at 2.6, 1.2, 0.7 and 0.2 Ma, possibly because of a stepwise weakening of the summer monsoon brought about by either further uplift of the northern parts of the Tibetan Plateau or increased global ice volumes[50], and the Tarim Basin may have reached its present size ca. 500 ka following uplift of the Kunlun and Tienshan Mountains[51-52]. In northern Xinjiang, NW China, the earliest loess on the Tienshan occurred ca. 800 ka, followed by further aridification and desert expansion ca. 650 and 500 ka[51]. In Central Asia, and unlike in China, the increase in loess deposition was progressive, and increased from ca. 7.8 cm/1000 years between 1.77 and 0. 85 Ma to 12.1 cm/1000 years from 0.85 to 0.25 ka, when it rose to 20 cm/1000 years[24, 53]. This trend probably reflects the increasing aridity of this region, and the expansion of the Kara Kum and Kizyl Kum deserts. The expansion of these deserts across Central Asia and north China created a near-continuous barrier that limited the northward expansion of hominins further south and restricted west-east dispersal (or vice versa) except when there were "windows of opportunity" in unusually mild interglacial periods.

One window that would have allowed hominins to enter North China from the west was between 580 and 380 ka. The sediment record from Lake Baikal, Siberia, for example, shows predominantly interglacial conditions during this interval, with a weakened MIS12 and MIS14, and no indication of mountain glaciation[54]. Hao et al.[55], suggested that "the extra-long NH [northern hemisphere] interglacial climate during MISs 15-13 provided favorable conditions for the second major dispersal episode of African hominins into Eurasia". Evidence for such a dispersal is provided by the hominin specimens from Dali and Jinnuishan, which several researchers have suggested should be classified as *H. heidlebergensis*[56-59]. It was probably through this opportunistic type of dispersal that some hominins between 580 and 380 ka introduced Acheulean assemblages into China across the Movius Line[32, 60].

2.3 Dispersals and source-sink models

Population response within an ebb and flow model can be modelled in terms of refugia, source and sink populations. In the context of human evolution, this type of model was first applied to Middle Pleistocene Europe[61, 62]. In cold periods, hominin and warm-tolerant animal species were confined to glacial refugia in the Iberian and Italian peninsulas, and SE Europe which contained the source populations of later expansion. When conditions improved, some groups moved northwards

and generated successive groups that expanded to the northern limit of the hominin range. These were sink populations in that they depended upon recruitment from groups further south to maintain viability (Fig. 3). The strength of this model was that it provided an explanation for the variability of the fossil hominins in Early and Middle Pleistocene Europe: climatic change provided the driving force behind the repeated dispersal, fragmentation and recombination of hominin groups, and also provided "windows of opportunity" in warm periods for immigration from Southwest Asia. Martinon-Torres et al.[21] later applied this model to Middle Pleistocene China, which, like Europe, has a variable fossil hominin record that does not show a simple unilinear evolution. Louys and Turner[63] also applied a source and sink model to East Asia and suggested that SE Asia was a potential refugium and source area for the sink populations in North China.

2.4 Dispersals and naïve faunas

Another approach that might help explain east-west movements is to consider the interaction between hominins and their prey fauna. I previously suggested that one reason why *H. erectus* dispersed eastwards across Asia was that that although much of the Eurasian fauna would have been familiar to hominins, hominins would initially have been wholly unfamiliar to the fauna[64]. Put another way, the Eurasian fauna would have been naïve as regards its awareness of the potential dangers posed by a bipedal, tool-making, carnivorous ape. (The same would also have applied to the main Japanese islands and the Philippines when these were colonised by *H. sapiens*).

Naïve prey face a steep learning curve in survival when confronted with an invasive predator such as wolf or humans. Although there are no regions left where the indigenous large-mammal fauna is unaware of the potential or actual threat posed by humans, there are examples from North America and northern Scandinavia of how recent faunas have reacted to the re-introduction of predators such as bear and wolf as conservation measures. Berger and colleagues[65] tested "naïve faunas" for their vigilance to predator cues versus the responses in "predator-savvy" populations (Fig. 4). They found that predator-savvy moose were far more alert than naïve ones to the sound and scent of bears and wolves, and to raven calls (because these birds scavenge the carcasses of moose that were killed by bears)[65]. The same researchers also showed that prey extinction is avoided because the prey populations quickly learn the importance of vigilance, and thereby becomes predator-savvy. Significantly, moose changed from being predator-naïve to -savvy in a single generation: they learnt to re-establish a "landscape of fear"[66].

Two points emerge from these findings. The first is that at the initial point of entry, Eurasian hominins had an advantage over their potential prey and carnivorous competitors because the naïve indigenous fauna was unaware of their abilities; and second, the easiest way for groups of *H. erectus* to maintain this advantage was to keep moving into new areas once the local fauna had become predator-savvy to them. This may help explain how *H. erectus* managed to disperse over a very large area despite its very low population size. The proposed model here is a type of "wave of advance" once proposed for the rapid expansion of modern humans into North America[68],
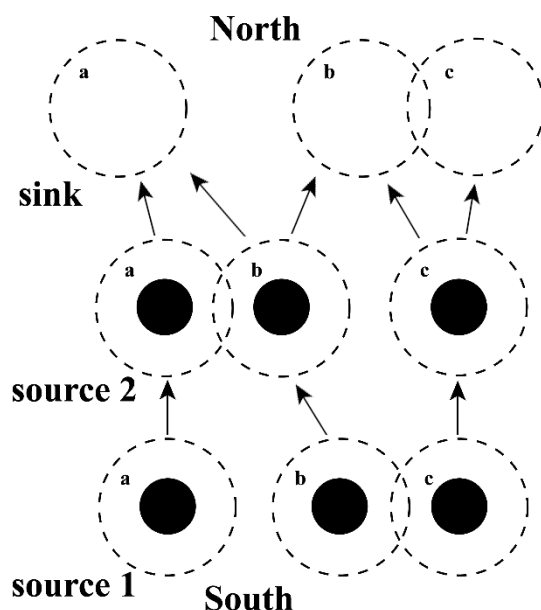
Fig. 3 Source and sink populations

Source and sink populations: Here, the bottom row indicates three metapopulations, or palaeodemes, in glacial refugia at the southern limit of the species' range. These are source populations that provide the basis for later expansion. The solid circles denote metapopulations during cold periods when populations contract into refugia; the dashed circles indicate interglacial or interstadial conditions when expansion from them is possible. Each is separated in glacial conditions, but in interglacial conditions, metapopulations b and c overlap. The middle row indicates how each expands in interglacial times and becomes a source population: here, metapopulations 2a and 2b overlap, but 2c (derived originally from demes b and c) remains isolated. The top row indicates the maximum expansion during an interglacial; here, deme 3a (derived from demes 2a and 2b) is isolated, but demes 3b and 3c overlap, although each has a different ancestry. At the northern edge of the species range, the metapopulations are sink populations in that they require recruitment from source populations to remain viable.

with its dramatic imagery of a "blitzkrieg" of humans targeting prey species that had no previous knowledge of the potentially lethal abilities of Homo sapiens. Here, the same ingredients are involved, but at much smaller scales of hominin group size and competence. No extinctions would have followed: the advantages to the hominin predator would have been short-lived; and it was unlikely any substantial increase in hominin populations occurred. Pott's suggestion[69] that the low density of artefacts at Yuanmou, China, might represent "a relatively brief stop by hominins as they passed through the area" is consistent with the proposed scenario of hominins moving from areas where the prey had become vigilant to new areas where the prey was still naïve.

The second implication is that if, as suggested by[67], prey populations can relax or even lose their vigilance in less than 10 generations, hominins could repeat their temporary advantage over potential prey by returning to areas where the prey had reverted from being predator-savvy to predator-naïve (Fig. 5). This way, hominins could still maintain viable local populations providing that they also practised a high degree of mobility. Because prey populations learn to be predator-savvy in only a few years, the advantage to humans would probably not last more than a
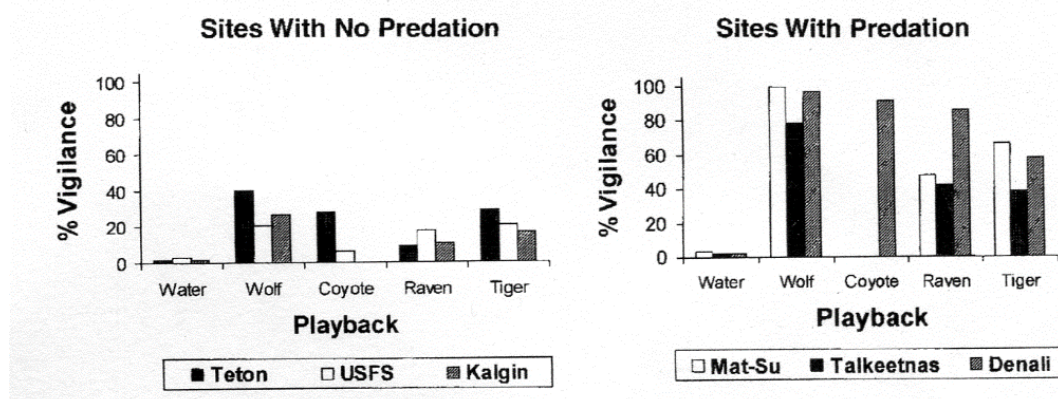
Fig. 4 Responses of moose to auditory predator cues among predator-naïve and -savvy herds.

Moose in areas where there was no predation were far less vigilant in their responses to the sounds of wolf, coyote and ravens (notable scavengers of predator kills) and even tiger than those in areas of predation. The sound of running water was used as a control in both groups[67]

few hunting seasons, but this could still be important in the initial phase of expansion.

Loss of vigilance amongst prey populations may also have been a major factor affecting the way hominins (and later, humans) recolonized regions that had been depopulated during glacial periods. Repeatedly through the Pleistocene, especially across the northern limits of the hominin range, from north China through Central Asia to West and Northwest Europe, hominin populations declined with each return to cold, dry (i.e., glacial) conditions, especially when winters were sub-freezing for prolonged periods. Crucially, however, in those areas where hominins either declined in number or disappeared, much of the resident fauna would have remained, or been replaced by, animals better adapted to the cold. Those animals that remained would have lost their vigilance regarding hominins, in the same way that moose in Sweden lost their vigilance against wolves when these became locally extinct (see above). Thus, when hominins were able to move northwards again when the climate improved, they would have encountered a naïve fauna, and thus recolonisation would have been easier – not just because of climate change, but because the prey was initially easier to kill. During the initial process of colonisation, they would have been at an advantage if they kept moving into areas where the prey fauna was naïve. A good example of where this process was likely repeated at the onset of each interstadial and interglacial is NW Europe, and the clearest and best documented example of this process is probably the region's re-colonisation in the final part of the last glacial period, during which humans moved back into the depopulated areas of northern Europe and ultimately colonised Britain, Scandinavia and the Baltic region. The same process might have operated when humans re-occupied the North China Plain after the LGM.

Predator competition might also have been a factor that at times inhibited dispersal. Turner[70] for example argued that hominins were largely excluded from Europe before the Middle Pleistocene because of competition with indigenous carnivores. In East Asia, the giant hyaenid

Pachycrocuta brevirostris may have impeded dispersal by *H. erectus* before it died out ca. 500 ka-ago[71]. It was, however, primarily a scavenger[72, 73] rather than a direct threat as a rival predator. Because hominins were repeatedly present on the Loess Plateau after 2.1 Ma-ago[28], and in the Nihewan Basin after 1.66 Ma-ago[33, 35], it might not have been a major deterrent to hominins despite opposing arguments by Binford and Stone[74] and Boaz et al.[75, 76]. Additionally, if hominins were "savvy" and not naïve about Pachycrocuta, they might easily have learnt avoidance strategies in the same way that moose learn to avoid wolves. By the Middle Pleistocene, hominins had probably emerged as the top predator in East Asia as well as in Europe and SW Asia[77].

2.5 Dispersal resulting from cultural adaptations

The remarkable range expansion of the genus Homo owes much to its ability to use know-how and material culture to extend its area of distribution. The ability to produce lots of sharp conchoidal flakes that could be used to strip meat from a carcass, cut wood, plants and skin probably underpinned the expansion of Homo erectus across Eurasia to an extent that would not otherwise have been possible for a small bipedal hominin. As argued above, its expansion across Eurasia would also have been facilitated by a prey fauna that was initially naïve. After 1.5 Ma ago in West Asia (but much later in East Asia), the development of bifacial and large cutting tools (LCT's) would have further benefitted *H. erectus*. In the Middle Pleistocene, the presence of *H. heidelbergensis* at Jinnuishan, Shandong Province, NE China, shows that this species had overcome many problems of over-wintering in harsh climates, and the development of wooden and later, stone-tipped spears, presumably made hunting safer and more effective[78].
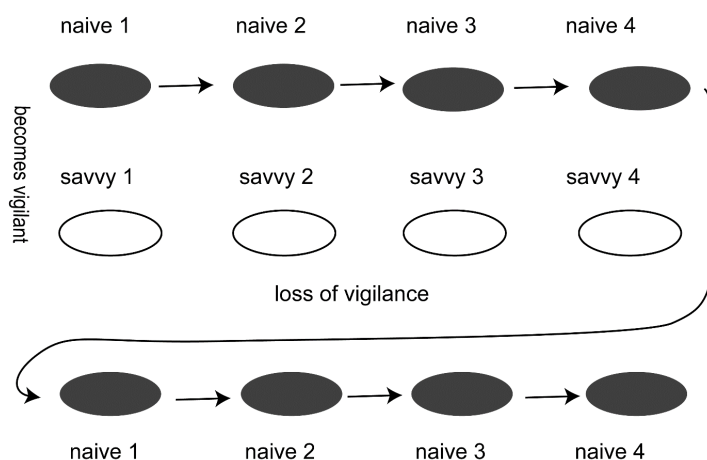
Fig. 5 Hominin dispersals in regions of predator-naïve and predator-savvy faunas

In this model, a hominin group targets four predator-naïve faunas in succession. Each fauna responds by becoming predator-savvy. However, over time, they lose vigilance and revert to being predator-naïve. At that point, the hominin group has the option of either moving to a new area with a naïve-fauna, or returning to one where a savvy fauna had lost its vigilance.

This type of dispersal may be applicable to H. erectus in continental Eurasia, to later hominins recolonizing an area vacated during a climatic downturn, and to late Pleistocene populations of H. sapiens when colonising regions such as Australia, island Southeast Asia, Japan and the Americas.

If the site of Kharganyn Gol 5, Mongolia, has Middle Palaeolithic artefacts in layers 6 and 7[79], Neanderthals or Denisovans were inhabiting an extremely harsh environment. In the last glacial cycle in European Russia, Neanderthals managed to extend their distribution up to 60°N. (roughly the latitude of Perm), where modern winters average -19°C, with 170-185 days of snow per year. Those conditions probably marked the limits of their ecological tolerance[80]. (The site of Byzovaia (65 °N, ca. 28 ka), which Slimak et al.[81] regarded as late Mousterian is Upper Palaeolithic[82]). It is also possible that Neanderthals dispersed into Inner Mongolia, North China, between 50 and 40 ka if we assume that they made the Mousterian assemblages at Jinnsitai[83]. If the mandible from Xiahe Cave is Denisovan[84] and its dating to 160 ka is confirmed, Denisovans 160 ka-ago were able to live in a very cold climate and at altitudes over 3,500 m above sea level, even if only seasonally. This is considerably higher than the Acheulean assemblage from Cona Cave, Georgia, which at 2,100 m above sea level was the highest Lower Palaeolithic site in Asia[12].

2.6 Dispersals by Homo sapiens

Homo sapiens was qualitatively different from other hominins in its ability to colonise areas that had never been inhabited by hominins, to colonise all regions already inhabited; and to eradicate all competitors. In those respects, humans have been incredibly successful as an invasive species.

Colonisation of new environments

East Asia shows better than any other area in the world how successful our species has been in inventing ways of colonising new environments. Four new environments were colonised: oceanic islands, the Arctic, rainforests and the Tibetan Plateau above 4,000 m a.s.l. Each can be considered in turn.

Dispersals by sea travel

Colonisation by sea voyaging is a classic example of a "jump dispersal", by which people (and also plants and animals) rapidly cross an area to reach a new place to settle (Fig. 6). This can be intentional or accidental. Intentional sea-faring requires the cognitive and technological abilities to build a sea-worthy boat or raft, provide it with food, fresh water and other provisions, and navigate it safely across open water. As seen below, there are numerous examples of maritime colonisation after 60 ka by *H. sapiens* that were almost certainly intentional. However, there are also claims that earlier hominins were also capable of intentional sea voyaging long before 60 ka. Morwood et al.[85], for example, when discussing the discovery of stone artefacts 800 ka-old on Flores, "conclude that *H. erectus* in this region was capable of repeated water crossings using watercraft". As the earliest evidence from Flores is now dated to 1.0 Ma[86], this evidence can also be seen as an even earlier example of intentional sea voyaging by *H. erectus*. Bednarik[87] asserted that "Navigation capability was apparently first developed between one million years and 800,000 years ago in Southeast Asia" and described the building of a raft with the type of simple tools found in Early Palaeolithic

assemblages. A crew of five later sailed it from Timor to Australia. However, the fact that *H. sapiens* today can build a raft with simple stone tools and sail it to a known destination does not necessarily imply that *H. erectus* had the cognitive and co-operative skills (or the impulse) to build a raft and sail into the unknown. On the other side of the world, the discovery on Crete of stone artefacts dated to the last interglacial or even earlier[88-90] and also Cyprus[91] has led to speculation of sea-voyaging in the Mediterranean long before *H. sapiens* appeared in Europe.

An alternative view is that these discoveries are examples of inadvertent oceanic dispersal. This type of colonisation is surprisingly common over geological time, and is probably the mechanism by which monkeys and other mammals[92] reached South America from Africa, or mammals on Madagascar[93, 94]. Simpson[95] 3) termed this type of dispersal as a "sweep stake", in the sense that only a few individuals were likely to be successful. The key point here is that "the longer a period of time in which a very rare event can occur, the more likely it is to do so"[96]. As Ruxton and Wilkinson[97] point out regarding Flores and other islands in Wallacea "while accidental arrival on an island would be merely improbable (for any particular island in any particular year). But given the large number of islands, tsunamis and river flood events, such colonisation might be quite likely to happen to at least some islands over a time period of archaeological interest".

The hominins that reached Flores, Indonesia 1 Ma-ago (and possibly several times thereafter[98]), and Luzon, the Philippines 700 ka-ago[99] are probably examples of inadvertent dispersal, and show that over long periods of time, some individuals drifting by accident will reach land. These accidental dispersals may have resulted from hominins floating on mats of vegetation detached from coastlines after a tsunami or cyclone[98, 100]. There are several recent examples of humans being swept out to sea on vegetation. Ruxton and Wilkinson[97] mention a woman rescued after clinging to driftwood for 80 km over six days after Hurricane Mitch in 1998, one individual rescued after five days and another after nine days after the 1995 Pacific tsunami of 1995, and a pregnant woman who drifted 100 km in seven days on floating vegetation after the 2002 Indonesian tsunami before rescue. As they note[97] "These anecdotal accounts clearly illustrate the possibility of individuals being washed up on remote islands following tsunamis and similar events". To reiterate the point that even if 99% of such events do not result in colonisation of an off-shore island, over tens and even hundreds of thousands of years, a few will. As Ihara et al.[101] concede after their simulation study of unplanned marine dispersal "The results of our simulations indicate that the accidental colonization hypothesis has limited plausibility, although it cannot be excluded as invalid".

Because hominins 100-200 ka-ago may have been capable of building and sailing a seaworthy boat or raft, it is harder to dismiss the possibility of intentional sea travel with the evidence for human presence at Talepu on Sulawesi 100-200 ka[102] and around the same time in Crete and possibly Cyprus. If that was the case, we might expect further similar evidence

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3)　Simpson (1940) also pointed out that dispersal by inadvertent drifting removed the need to postulate the existence of land bridges that allowed some (but not all) species to cross to the new region and then conveniently disappeared.
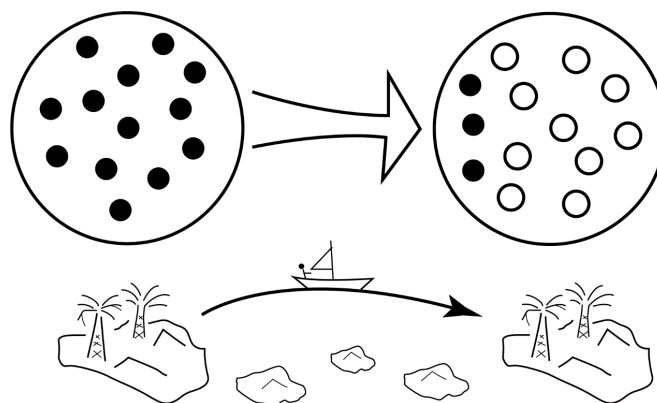
Fig. 6 Jump dispersal

This diagram shows bold colonization by jump dispersal. Here, some groups (A, black circles) at the edge of an island metapopulation take the risk of jumping past a series of unproductive islands to find a better island (B) than their present location. Although the risk of failure is high, success means that a new region can be colonized by descendant groups (white circles). Jump dispersals can also happen on land, as when people "jump" from one oasis to another when crossing a desert.

from islands such as Malta, Corsica and Sardinia in the Mediterranean, or Timor and Lombok in Wallacea. Nevertheless, an alternative scenario is that hominins were building boats 100-200 ka-ago that were used close to the shore, but occasionally some were blown out to sea and a few inadvertently landed on an island. At present, it is not possible to provide a definite answer to when intentional sea faring first began.

On current evidence, intentional sea voyaging appears unique to *H. sapiens* and resulted in East Asia in the colonisation of Sahul – the conjoined landmass of Australia, New Guinea and Tasmania – Wallacea – the islands between Java/Borneo and Sahul – the main Japanese islands, the Ryuku Islands between Taiwan and southern Japan, the Philippines, the Kurile and Aleutian Islands and possibly coastal North America. Sahul – the conjoined landmass of Australia, New Guinea and Tasmania – was reached by 50 – 55 ka[103] (and possibly as early as 65 ka if one accepts the dates and associated material from Madjedbebe rock shelter[104]). The fact that Australia was reached by 50-55 ka means that the main colonisation of Wallacea had to begin by that time, although the oldest evidence from this region dates from 43,283 - 44,631 cal BP at Laili, Timor[105]. The discrepancy may be an artefact of dating techniques, as the earliest dates from Wallacea are from C14, but the earliest Australian dates were obtained from OSL. The extinction of *H. floresiensis* at Liang Bua, Flores, at ca. 50 ka may imply that *H. sapiens* arrived at that time. Fishing for tuna and other pelagic fish is evidenced at Jerimalai, Timor, by 42 ka[106].

The Japanese Islands were another region that could only have been colonised by sea crossings. The shortest and most direct route is across the Tsushima Strait, which was reduced from ca. 100 km width to ca. 20 km during the LGM[107], but colonists may also have arrived from the coasts of South China, Siberia, or via the Ryuku Islands[108]. The earliest site on PalaeoHonshu

– the conjoined islands of Honshu, Kyushu and Shikoku – is Idemaruyama and is dated at ca. 38 ka and its inhabitants used obsidian from the island of Kozushima, at least 45 km off-shore[109]. Okinawa in the Ryuku Islands between Taiwan and Kyushu was colonised by 36,000 years ago. It was probably reached by sailing from Taiwan because the powerful north-flowing Kurishio Current would have made sailing south from Kyushu extremely difficult. Reaching Okinawa was particularly difficult because it involved crossing 105 km of open water between Taiwan and the nearest island of Yonaguni, and at least 220 km of open water between the southern and central Ryuku Islands. (Interestingly, a reed boat was successfully paddled from Taiwan to Yonaguni in 45 hours in 2019[110]. The evidence from Okinawa is also important in showing the world's earliest example of a species being translocated by humans: at the cave of Sakatari, layer 2, dated at 19,635 to 23,425 cal BP, has evidence of pig (Sus scrofa), which was not native to the island but had to be introduced[111, 112]. This translocation involved considerable foresight in allowing pigs to breed on the island and not eating them on arrival. It is not yet clear when Luzon in the Philippines was colonised by our species but was probably after 52 ka, when *H. luzonensis* is recorded[113].

North America may also have been reached by sea along the "kelp highway" of the Kurile and Aleutian Islands that lie south and north of the Kamchatka Peninsula. Although Beringia is usually regarded as the most likely region from which humans reached North America, the rich marine environments along the coast of northeast Siberia, and the proven ability of humans to undertake sea voyaging in East Asia by the end of the Pleistocene make a maritime route a plausible scenario for the colonisation of North America[114, 115].

There is so much that we do not yet know about these first sea voyagers - in particular, whether their boats were made from reed, skin, bark or wood; the communities (now submerged) that made and used them; their reliance upon marine resources for their subsistence; their source populations; and how some coastal communities in East Asia were able to grow sufficiently large to be able to create an emigrant population that colonized the Japanese islands and the Philippines. Regarding Sahul, it was not colonised by accident as an unplanned one-way trip, but most likely as a result of planned migration involving numerous groups and numerous return voyages[116] by several boat loads totalling perhaps 1,000-2,000 people for mainland Australia[117]. In a recent simulation study, Bradshaw et al.[118] suggest a founding population of between 1,300 and 1,550 individuals who could have arrived after one voyage, or (perhaps more likely) through several voyages of ca. 130 people over 700-900 years. (And perhaps even more likely, by numerous voyages of small groups (perhaps only a dozen or so) over several centuries. These estimates imply that the coastal regions of Sunda, mainland Southeast Asia and China had communities that were large enough to send overseas substantial numbers of people, albeit most likely in small groups over several centuries. Sadly, we know nothing about them because they existed when sea levels were 40-60 m below present levels.

Dispersals into the Arctic

Humans were probably hunting mammoths inside the Arctic Circle before 40,000 years ago,

when sea levels were 50-80 m below present levels. At Sopochnaya Karga (the SK site), at 71° N, the skeleton of a mammoth, dated at c.40-45 ka BP, was found that showed injuries before death and cut-marked bone[119, 120]. Two ribs had a notch-like lesion consistent with ones caused by spears, and post-mortem damage was also evident on the tip of one tusk and the mandible. There is also an assemblage from the site of Bunge-Toll 1885, where remains of woolly mammoth, woolly rhinoceros and bison were found, as well as a wolf humerus that had a puncture-cut wound that was likely caused by a human projectile. The humerus was dated to 44, 650 + 950/-700 BP, which is close in age to a date of 47,600 +2600/-2000 BP for the mammoth remains[120]. Although it is uncertain whether these two sites denote rare events or were already part of a regular pattern of mammoth hunting by humans in the Far North, they imply that humans 40,000 years ago were hunting much further north than Neandertals appear to have managed. Conclusive evidence of mammoth hunting comes from the site known as Yana RHS (rhino horn site) and the nearby Yana Mass Accumulation of Mammoth (YMAM) site. These also lie at 71° N. and were used on at least three occasions between 27,000 and 29,000 years ago[121, 122].

Although we have a basic outline of when humans first colonised the Arctic, there is still much we need to understand. One issue is whether they had domestic dogs 30,000 years ago, as argued by some[123-126], but doubted by others[127, 128]; another is how people moved over frozen landscapes by skis, sleds, and snowshoes. We also need to learn more about the social networks that would have been critically important in the harsh landscapes of the Arctic, and which may have been the means by which anthraxolite (a soft black rock) was present at Yana 600 km from its source in the New Siberian Islands[129]. Ethnographic sources and experimental archaeology would also lead to better understanding of how clothing was made, and fire was used in a largely treeless landscape. One interesting clue is that the lack of wear on the toe bones of the 40 ka-old Tianyuandong individual may provide the earliest evidence for the habitual use of footwear[130].

Dispersals into rainforest

Homo sapiens was probably the first hominin to adapt to rainforests[131].

These were arguably the most challenging of the environments in East Asia that were colonised for the first time, Animals that were large enough to be worth hunting tended to be largely solitary or lived in small groups (Tab. 1); those living on the ground were often difficult to see and track, and pursuing them was impeded by dense vegetation, and those (such as monkeys) that lived in the high canopy were even more difficult to hunt. With plants, it is necessary to know which can be eaten, and at what time of year, and whether it is the roots (as with tubers such as yams), stems or fruits that are edible; some are poisonous when picked and require processing by washing or boiling before they can be eaten. Rainforests can also be unhealthy places to live because of water- or insect-borne diseases since open wounds can easily fester and because much of the smaller fauna can be venomous. Although rainforests have been described as the world's largest natural pharmacy, great skill and knowledge is required in knowing what plants (and which parts of them) can serve as medicines, and how these can be used. Xhauflair

et al.[132] observed that inhabitants of Palawan used 95 plant species, and quote Conklin who recorded over 1,100 species of usable plants among the Huannóo of Mindoro in the Philippines. For humans to adapt to living in rainforests was thus a major achievement, particularly for a creature that originated and long flourished in grasslands and open woodlands.

The earliest clear evidence of humans in rainforest is from Lida Ajer, Sumatra, where two human teeth were found in an assemblage largely consisting of orangutan, and dated at 65-73 ka[133]. Evidence from Niah Cave, Borneo, shows that it was first occupied ca. 50 ka-ago. The *H. sapiens* cranium is dated to ca. 45-39 ka cal BP. Humans were hunting bearded pig (29%), orangutan (6%) and leaf monkeys that are both terrestrial and arboreal (16%). There is evidence from starch grains of deep-rooted yam (Dioscorea hispida and Dioscorea spp.) and sago palm (Caryota mitis or Eugeissona spp.) at 48 ka cal. BP. These are particularly interesting because they need detoxifying before they are edible. According to Barker and colleagues[134], a piece of Dioscorea hispida the size of an apple can be fatal if eaten raw. Seeds of Pangium edule were also found; in ethnographic contexts, the hydrocyanic acid in these nuts could be removed by burying the ripe fruits or boiled seeds in a pit for 10-14 days and then boiling them, or by burying the seeds with ash for up to 40 days[134]. In the cave, there are pits containing nut fragments dated at 39 ka and 35 ka that may have been used for detoxifying nuts.

There is also evidence of deliberate forest burning to create or enlarge open spaces that would provide edible tubers and other plant foods, and for trapping those animals attracted to such patches. High frequencies of pollen of Justicia – a coloniser of burned areas – consistently occur in forest phases. This evidence is consistent with high frequencies of charcoal fragments in pollen cores from the Sulu Sea north of Borneo and dating back 50,000 years, and possibly an indicator of when our species arrived in the region and began to modify their surroundings. According to Hunt and colleagues[135, 136] study of the local vegetation at Niah, the vegetation was cyclic, and varied between lowland and montane forest, and more open savannah-like environments indicating lower temperatures and rainfall compared with the present day. The interesting point here is that people may have reached the site ca. 50 ka during a climatic phase when habitats were fairly open, and biomass burning may have taken place during more forest-rich phases as a way of creating or enlarging open spaces; people were not therefore necessarily foraging under closed canopy high forest[135].

Humans were also living wholly in rainforests in Sri Lanka before 40 ka BP. Excavations of the caves of Batadomba lena, Fa-Hien lena and Kitulgala lena have produced remains of *H. sapiens* associated with a microlithic assemblage[137, 138] and an extensive bone industry that included points that were probably used as projectiles or in snares as early as 36 to 38 ka BP[139]. Faunal data indicates that semi-arboreal and arboreal primates comprise most of the mammalian assemblages; other resources exploited at Batadomba-lena include mouse deer, giant squirrel, mongoose, jungle cat and civet, as well as Canarium sp. nuts and starchy rainforest plants[139], all of which imply dedicated rainforest subsistence. Roberts and colleagues[140] showed from stable carbon and oxygen isotopic analysis of human and other animal bones from these caves

that human diet was overwhelmingly from rainforest foods. This lifestyle was maintained from 38 ka BP through the rest of the Pleistocene (including the last glacial maximum) and into the Holocene up to when agriculture was introduced c. 3000 years ago. The rainforests of Sri Lanka were therefore not only a resource zone but also a refugium during the last glacial maximum.

Xiaodong in Yunnan Province in southwest China has the earliest Hoabhinian assemblage – another link to southeast Asia – that is dated to 45 ka[141]. Because this site lies in rainforest, this site may indicate the earliest colonisation of rainforest in mainland southeast Asia. There is still much to learn from this site and others in SE Asia and the Philippines about the range and type of plant and animal foods, and the type of social networks that linked groups in this resource-rich but challenging environment.

Dispersal onto the Tibetan Plateau

The excavation of a blade assemblage at Nwya Devu[36, 37] shows that humans were living at 4600 m asl. as early as 30000-40000 years ago. This discovery implies that by that time people were able to cope with hypoxia – illness caused by a shortage of oxygen – as well as extreme winter cold. Huerta-Sánchez et al.[142] have suggested that this ability may have been derived from Denisovan-like DNA. As the Xiahe mandible, found at 3,600 m asl on the north-east part of the Tibetan Plateau, is attributed to a Denisovan, the earliest inhabitants of the Plateau may have been Denisovan who interbred with *H. sapiens* after 40,000 years ago. Further a DNA analysis is needed to elucidate the demographic history of this region.

Tab. 1 Summary of differences between the Palearctic and Oriental Realms of China and neighbouring regions

	Continental East Asia	South China and SE Asia
Biogeographic realm	Palearctic	Oriental
Climate	cool/cold, dry; sub-freezing winters	warm, wet; warm winters
Rainfall	largely winter	monsoonal; summer
Plant foods	scarce and seasonal	abundant year round
Animal foods	herd and migratory (e.g. horse, gazelle)	small groups or solitary; localised
Subsistence	highly mobile if dependent on terrestrial resources	mobile but usually with small annual territories
Population size and density	small, dispersed if dependent on terrestrial resources; possibly larger if dependent on coastal resources	usually larger and less dispersed
Level of risk	high	lower
Type of clothing	clothing – hide/fur	optional, or plant based
Regional occupation records	often discontinuous	more likely continuous
Raw materials	sometimes obtained over large distances	usually local
1st appearance of *H. sapiens*	45-40 ka BP	Possibly as early as 80-100 ka BP

2.7 Dispersals, colonisation and population dynamics

The main issues here are the colonisation of abandoned environments and ones already inhabited by other types of hominins.

Colonisation of abandoned environments

There are three examples from North China of humans colonising environments that had been abandoned. On an ebb and flow model, these areas would have been abandoned because their inhabitants moved south towards refugia in the Qinling Mountains when the climate deteriorated. The resulting vacuum was filled by people adapted to cold conditions coming in from the north. The first is evidence that Neandertals may have expanded ca. 47-42 ka eastwards into Inner Mongolia, ca. 2000 km east of the previously recorded easternmost location in the Altai region of Siberia[83]. The second immigration event is evident in the Shuidonggou (SDG) site cluster. The lower cultural layer of SDG 1 contains an IUP (initial upper palaeolithic) blade-based technology produced by Levallois and prismatic methods of core reduction dated to ca. 43 ka[143] and similar in age and composition to the IUP assemblages seen in the Altai Mountains and Mongolia. The individual from Tianyuandong, dated at 40328 ± 816 ka BP calibrated[144] may have been part of this immigration event.

The third immigration event into north China is evidenced by the late glacial microblade industry which probably originated in Siberia and appeared in north China at sites such as Youfang ca. 26-29 ka[145] and Longwangshan ca. 27-25 ka cal. BP[146] and ultimately spread as far south as Lingjing in Central China[147].

Colonisation of inhabited environments

The study of hominin palaeo-demography in the eastern part of Asia is complicated by the fact that it was inhabited by several types of hominins in the Middle and Upper Pleistocene prior to the arrival of *H. sapiens*: in continental Asia, *H. erectus*, *H. heidelbergensis*, Neanderthals and Denisovans; *H. luzonensis* in the Philippines, and *H. floresiensis* on Flores. By 50,000 years ago, *H. sapiens* was the sole resident. We therefore need to consider the role of immigration, and population assimilation and replacement.

Colonisation through assimilation of the indigenous population

On some occasions, parts of a metapopulation began to invade an area that was occupied by a different type of hominin. The invasive metapopulation then proceeded to assimilate the females of reproductive age, thus degrading the previous viability of the indigenous population (Fig. 7). This type of scenario is indicated by evidence of gene flow from Neandertals and Denisovans into Homo sapiens outside Africa, and resulting in an "interbreeding bonanza"[148] between *H. sapiens*, Neandertals and Denisovans. Although we will never know the nature of these encounters between *H. sapiens* and Neandertals, their long-term consequences may have been either negative (such as male hybrid infertility[149]), or positive if leading to "hybrid vigour", enhanced immunity[150], and the acquisition of beneficial genes such as those that facilitated life

at high altitudes such as the Tibetan Plateau[142] or in cold environments.

Colonisation through population replacement

Although it used to be widely thought that *H. sapiens* replaced all of its contemporary hominins such as Neanderthals and Denisovans, total replacement without any interbreeding was in fact rare. In East Asia, only two populations were completely replaced by the arrival of *H. sapiens* at ca. 50 ka, and both were small and localised. The first was *H. luzonensis* in the Philippines, and the second, *H. floresiensis* on Flores. Both were island populations that had been isolated for a long time and were particularly vulnerable to an invasive predator. These hominins were small, probably had only a rudimentary technology, and above all, were naïve in that they had no prior experience of Homo sapiens. They were in the equivalent position of the dodo on Mauritius that became extinct within a century after the arrival of humans. Their extinction would not necessarily have been violent as it would have been sufficient for *H. sapiens* to appropriate their foraging grounds and displace them to marginal habitats.

Dispersals and social networks

Hominin (including human) dispersals can take place without a complex social network, as when a community relocates to a new area, or part of it forms a new or daughter community.

Rather than individual groups entering, learning about and using a new niche, a hominin that was socially complex and linguistically competent[151, 152] could operate as part of an integrated network of groups, each of which could operate independently but maintain links that would allow sharing of information over a large area. Successful networks would operate with a high degree of mutual reciprocity, so that risks could be pooled: groups would operate within a support network so that individuals could rely on neighbouring groups if they encountered local adversity.

Networked dispersals are probably unique to *H. sapiens* and probably under-pinned the maritime colonisation of Wallacea, Australia, the Japanese and Ryuku Islands, the Philippines and perhaps the Americas as these require the skills, materials, people and information of several communities[64]. Effective networks would also have been essential when humans dispersed into Transbaikalia, Mongolia and North China, where winters were harsh, and main prey species were horse and gazelle that are migratory and have enormous annual territories of up to 30000 km^2 [153-154]. High mobility and high unpredictability of prey species and climate would have provided strong incentives for groups to operate as part of a social network as a way of minimising risk.

Evidence of palaeolithic networks is elusive, but a good example is the distribution of beads from the Altai through Transbaikalia, Mongolia and North China in the IUP[155]. An important unifying characteristic of this region is the use of ostrich egg shell beads and pendants made from animal teeth, as well as the occasional use of ochre. These first appear in Transbaikalia ca. 42–45 ka[156-158], and ca. 40–42 ka in the Tolbor Valley of northern Mongolia[159-162]. The ornaments from Upper Cave, Zhoukoudian, are most like those from Denisova, and both assemblages include perforated canine teeth of various types of deer and small carnivores, round beads, bone
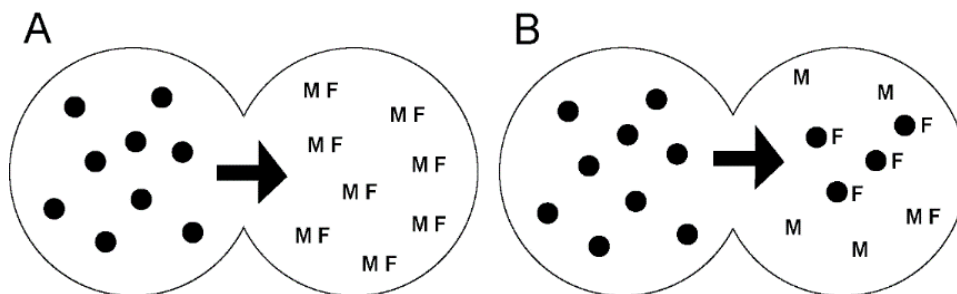
Fig. 7 Colonisation by assimilation

In this scenario, part of a metapopulation (A; black circles) begins to invade an area occupied by a different type of hominin, shown as MF, with M = males and F = females. The invasive metapopulation then proceeds to assimilate the females of reproductive age (B), thus degrading the previous viability of the indigenous population. This type of scenario is indicated by evidence of gene flow from Neanderthals and Denisovans into Homo sapiens in Siberia and may also help explain the evidence for hybridization in the East Asian skeletal evidence.

pendants, and perforated shells, none of which are found in south China but are widespread across Mongolia and southern Siberia[155, 158]. The hunting groups in this enormous region would have been part of an extensive network of groups that operated over an enormous territory in pursuit of highly mobile and often unpredictable migratory prey such as horse and gazelle.

Other examples from East Asia are the long-distance exchange networks in obsidian in NE Asia (Japan, Korea, China, eastern Siberia) after 40 ka, with some obsidian transported 600 km by sea between Hokkaido and Kamchatka, and up to 1000 km from Japan into Siberia[163, 164]; and anthraxolite at Yana that came from 600 km away[129].

3 Discussion: an outline hominin biogeography of East Asia

Hominin dispersals are the outcome of processes that are usually multi-facetted, and are only rarely explained by a single model or variable. There are also profound differences in the types of dispersals undertaken by *H. sapiens* and earlier hominins. The main types of dispersals that occurred in East Asia in the Early and Middle Pleistocene are summarised in Fig. 8-9. In the Palearctic Realm of continental Eurasia, climatic change was the main driver, with the repeated alternation of cold and dry, and warm and moist periods of the Pleistocene. With the sparse data available for the Early and Middle Pleistocene, a simple ebb and flow model is an appropriate way of showing how hominins moved north when the climate permitted, and retreated south or become extinct at the limits of their range when the climate deteriorated. In the case of China, the hominin skeletal record is sufficiently detailed to allow the identification of palaeodemes and a source-sink model offers greater insights into explaining that complexity.

Dispersals west to east (or vice versa) in the Palearctic Realm of East Asia can be modelled in several ways. The climatic changes that determined movements north to south would also

have created corridors that permitted west-east movements if arid regions became grassland, or barriers that prevented such movement if grasslands became desert. Hominin expansion across continental Asia can also be explained as simple range expansion by a "creep and crawl" model of gradual dispersal, or by a more dynamic process in which hominins searched out prey faunas that were initially naïve and easier to hunt.

For the Oriental Realm of South China and SE Asia, the two main factors that underpinned hominin dispersals in the Early and Middle Pleistocene were the repeated fragmentation and recombination of rainforest that opened up or closed down corridors of more open vegetation, and changes in sea level that exposed or drowned land in coastal regions. These changes in sea level had far greater consequences in the continental parts of the Oriental Realm, particularly on the Sunda Shelf and the South China Sea than in the sub-Realm of Wallacea, where changes in sea level did not alter the basic geography of the region. As example, when sea levels were 50 metres below present levels, the islands of Borneo, Sumatra and Java were conjoined to each other and the Asian mainland, whereas the site of Jerimalai on Timor that is now within one kilometre of the coast was still usable as a base for fishing 42000 years ago when sea levels were
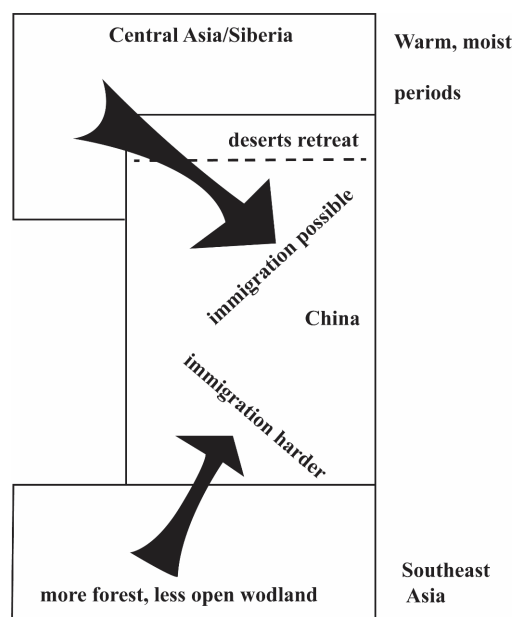
Fig. 8 Model of immigration into China in warm periods

In warm, moist periods, the desert boundary retreated and immigration into north China was possible from regions to the north and west. In south China, immigration from southeast Asia might have been more difficult because of the expansion of rain forest. Source: the author
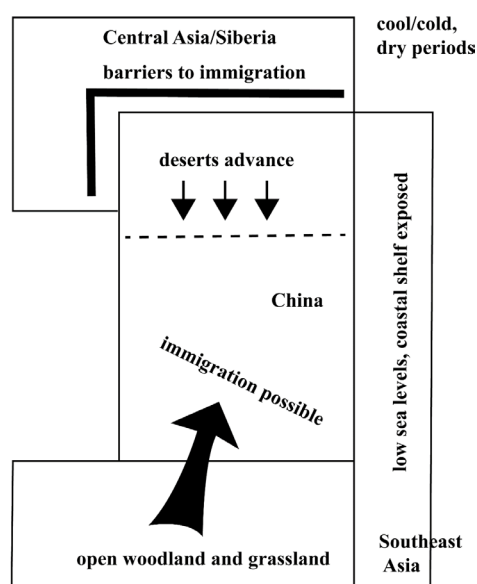
Fig. 9 Model of immigration into China in cold periods

In cold, dry periods, the desert boundary shifted southwards in north China, and immigration from regions to the north and west would have become more difficult. On the other hand, the contraction of rain forest and expansion of open woodland and grassland in south China would have facilitated immigration from southwest Asia. In addition, the fall in sea levels exposed more land and opened up possibilities for colonisation. Source: the author

ca. 50m lower[165]. Coastline bathymetry was also important. The post-glacial rise in sea level drowned 84% of the island of Palawan north of Borneo[166], but hardly affected the coastlines of many Wallacean islands[165]. As Kealy et al.[167] point out, the main consequence of rises and falls in sea level in Wallacea were their effects on inter-island visibility. Additionally, there is the factor of oceanic drift that probably resulted in the accidental dispersal of *H. floresiensis* and *H. luzonensis* (and their associated fauna) to Flores and Luzon respectively.

Dispersals in East Asia after ca. 70 ka by *H. sapiens* (Fig. 10) were very different, and were driven by innovations that occurred more rapidly and were more far-reaching than those of earlier hominins. The main innovation that occurred in both the Palearctic and Oriental Realms was the ability to colonise off-shore islands such as those of Wallacea, PalaeoHonshu, the Philippines, the Ryukus islands and Sahul by a series of jump dispersals involving complex, inter-connected networks and probably hundreds of individuals. As Sahul was colonised by 50-55 ka (and perhaps earlier), seafaring must have begun earlier in SE Asia and Wallacea. In the Oriental Realm, humans were learning how to inhabit rainforest by 63-73 ka in Sumatra, and by 50 ka in Borneo and probably around the same time in South China. In the Palearctic Realm, humans learnt how to inhabit regions of extreme cold and thereby colonised the Arctic as well as eastern Siberia and Mongolia, and the high Tibetan Plateau above 4000 m by 30 ka. This new-found ability to inhabit cold and harsh environments such as Mongolia also enabled humans to repeatedly move southwards into North China and occupy a landscape that had been abandoned by communities whose source populations were further south in the valley basins of the Qingling Mountains and Yangtse Valley.

The other important issue involved in dispersals after 50 ka is the interaction between *H. sapiens* and its contemporaries. Genetic evidence indicates that assimilation was the main outcome of contact between
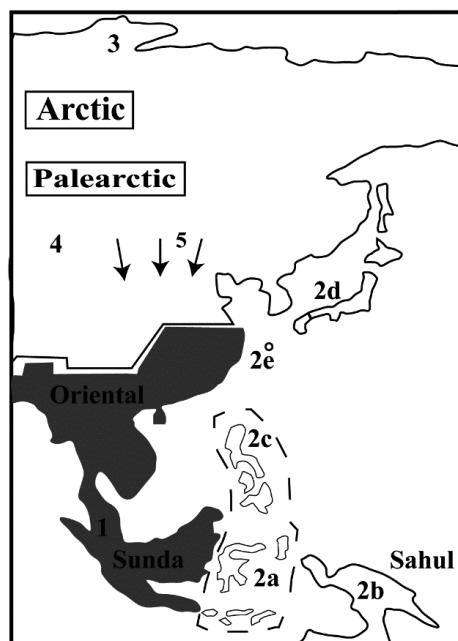
Fig. 10 Human dispersals in East Asia after 70 ka

There were 5 major dispersal events in East Asia by H. sapiens after 70000 years ago:

1: dispersal in the Oriental Realm into rain forest in Sumatra (Lida Ajer) and Borneo (Niah cave) and possibly South China (Xaiodong); 2: a series of jump dispersals to off-shore islands: 2a, Wallacea; 2b, 2b, Sahul; 2c, the Philippines; 2d, PalaeoHonshu (the conjoined islands of Kyusho, Honshu and Shikoku); 2e, Okinawa and the other Ryuku islands; 3, the high Arctic (Yana, Sopochnaya Karga); 4, the Tibetan Plateau above 4,000 m. asl.; and 5; dispersals into North China from Mongolia and south Siberia (SDG 1 and later. the microblade tradition) by cold-adapted groups. These dispersal events were in addition to the previous pattern of ebb-and-flow in the Loess Plateau by communities whose source populations were further south.

humans, Neanderthals and Denisovans. Total replacement affected only the isolated island populations of *H. floresiensis* and *H. luzonensis* on Flores and Luzon respectively.

4 Concluding statement

A focus on dispersals opens a wide range of doors through which we can investigate the palaeolithic record of regions such as East Asia. A biogeographic perspective requires consideration of the prevailing climate, vegetation, relief and type of terrain, as well as the way the climatic changes of the Pleistocene would have created corridors for or barriers to dispersal. Hominin dispersals can also be better understood if we assess the nature of their prey, and whether it was naïve or vigilant when encountering hominin hunters. The extraordinary dispersals by our species into rainforests, across open seas to off-shore islands, to the Arctic or the highest parts of the Tibetan Plateau necessitate examining the types of technical, social and cognitive adaptations that made those dispersals possible. East Asia is particularly suitable for these types of studies because of its diversity of landscapes and adaptations of its inhabitants.

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