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To what extent (if any) climate shaped the evolutionary history of our own genus and affected early hominin behaviour and dispersal? Searching for an answer to a hotly debated question

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FIRST PARAGRAPH: It is widely accepted that our own *Homo* genus originated sometime around the Pliocene/Pleistocene boundary in Africa. *Homo* remains are first reported at about 2.34 Ma [1], but archaeological evidence at Gona, in Ethiopia, may indicate an earlier appearance of this taxon from around 2.6 Ma [2]. Although scholars disagree as to the ancestor of the human clade, it could rationally be expected that, as a primate, this ancestor was in some way ecologically dependent on arboreal environments, particularly woodlands. Thereby, it has long been assumed that human evolution was primarily linked to a general cooling trend accompanied by increasing aridity and seasonality, which the Earth's climate system experienced around the Middle Miocene, intensifying during the later Pliocene and Pleistocene [3]. For instance, Vrba [4], analysing biotic changes and hominid evolutionary events in Africa during this time, suggested a number of hypotheses and predictions that link the climatic changes towards cooler, more arid and open environments, to the main events in hominid evolution, including the "massive geographical expansion of "*Homo erectus*". Moreover, climate changes are thought to have exerted selective pressures, favouring large brains and cultural evolution [5-7], and, according to the 'Variability Selection Hypothesis', significant aspects of hominin evolution (bipedality, brain expansion, stone tool production as well as migration and dispersal) would have been promoted by amplified long-term climate fluctuations [8-10].

气候对真人属进化史及早期人类行为和扩散有否影响及其程度：探索此热点问题的答案

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首节：众所周知，在上新世更新世分界时，我们人类在非洲起源。在早期报道中人类遗迹最早可追溯至 234 万年前[1]，然而埃塞俄比亚的戈纳地区的考古学证据却可能将人类出现的时间推至约 260 万年前 [2]。尽管学者们在人类的祖先是什么的问题上莫衷一是，但我们的祖先作为灵长类，那么从生态学角度考虑，多树的环境，特别是森林地带，在一定程度上是其赖以生存所必需的。因而，一直以来我们认为人类进化是和中新世的气候环境紧密联系的，中新世时全球逐渐变冷，并伴随着干旱加剧和季节性增强，而这一趋势又在上新世晚期和更新世被加强 [3]。例如，在分析了上述时期发生在非洲的生物变化和人类进化事件后，Vrba[4]提出一系列的假说和预测：当时，气候逐渐变冷，雨量减少，干旱接踵而至，茂密的森林逐渐稀疏以至大部分消失，剩下了大片的开阔空地，这些环境的变化是与人类进化的重大事件包括"直立人地理上大规模扩散"等相联系。另外，有研究发现气候变化作为选择压力使人类脑容量增大，并促进了文化的不断进步 [5-7]。而且，根据"变异选择假说"，长周期气候波动促进了人类进化的某些重大进展(两足行走、脑容量增大、石器工具的生产、迁徙和分布等)的出现 [8-10]。

A glance at Africa

Most recently, environmental factors which may have triggered evolutionary transitions in African hominids, have been widely explored, roughly supporting, at least as regards East Africa, an average scenario characterised by significant vegetation change at about 2.5 Ma, when, coinciding with global climate change, arid grasslands expanded into the lowlands while highland vegetation was found at much lower elevations[11]. Researchers have also been focusing on short timescale ecosystem fluctuations, driven by astronomically-forced global climate changes, as well as on local to continental geographical factors that might have affected vegetation cover differently. The resulting complex pattern of habitat heterogeneity might have represented a highly dynamic environmental context in space and time for early hominin

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evolution [12-16]. Evidence from isotope analyses of pedogenic carbonates and tooth enamel of ungulates, confirms the presence in East Africa, during the Early Pleistocene, of grassland-dominated ecosystems and suggests that by 2.0 Ma, early *Homo* was able to extract resources from a broad spectrum of habitats ranging from open grassland to riparian forest [17].

From Africa towards Eurasia: who, when, where, and why?

Although our knowledge of the environmental context in which African hominins originated and evolved have dramatically increased during the last couple of decades, the actual role played by climate in driving/triggering the time and mode of hominin dispersals from Africa towards Eurasia and how it may have coincided with very few other African mammals, as would be expected following a "migratory wave scenario"[18-19], is still a matter of debate.

The role of climate change in promoting faunal evolution and functional turnovers is, indeed, a hot topic in palaeobiology and palaeoecology. The challenge is to ascertain the impact of environmental factors on dispersals of small and large mammals, including hominins. Over time, ecologists and evolutionists have been widely divided as to whether progressive changes in the composition of mammal faunal complexes (fluctuations in biodiversity, biomass, and ecological structure of palaeocommunities) might be interpreted as a mere response to climate change [20-24] or as the result of intrinsic biotic factors that exert an important control on faunal renewal[25-27]. Actually, the cause- and effect-relationship between climatic oscillations and faunal changes may be the cumulative result of the responses of individual species, which could have affected the internal dynamics of communities. Moreover, climate change may have removed keystone species, causing changes in interactions among species and causing ecosystems to reconstruct [28]. Thus, climate (e.g changes in the Earth's climate system at about 2.6 and 1.0 Ma) appear to be a critical factor in triggering faunal renewals, but, intrinsic biological factors (competition/coevolution) could have influenced the timing and the extent of the subsequent structural rebuilding of faunal complexes (which did not necessarily reflect a strict dependence on astronomically forced climate shifts) and may also have been essential in determining faunal complex evolution.

At middle latitudes, mammals generally reacted to climate changes not by simply evolving and producing new species or becoming extinct, but also by varying their ranges, in agreement with changes in the vegetation cover and latitudinal displacement of biomes, leading to discrete dispersal bioevents as a response by individual species to environmental disturbances[29]. All in all, climate change, via migrations and dispersal events, caused diversity to increase but altered palaeocommunity equilibria, leading to new intra- and inter-guild dynamics and progressive shifts in the taxonomical composition and ecological structure of the faunal complexes. Accordingly, internal dynamics and changes in competitive relationships may have played an important role in the evolution of mammalian communities [29,30].

But what was the impact of climate on hominin dispersals and their successful settlement in Eurasia, particularly in the Western Mediterranean, during the Pleistocene? What were the causes that promoted such dispersals? Did hominin dispersals coincide with those of other mammalian taxa?

Although recently, interest in the debate has increased and a number of different patterns have continuously been proposed to explain the time and mode of the "out of Africa" dispersal/s [31-35], several points as regards "who, when, where, why, and how" need to be clarified before confidently answering the question as to whether Pleistocene climate and environmental changes played a special role in triggering movements between and across Africa and Eurasia.

New data, on the one hand, enable us to answer the question as to "who" was the earliest hominin to move from Africa to Eurasia and which dispersal routes they might have followed. On the other hand, it forces us to question models previously proposed, explaining the reasons why early *Homo* dispersed to and settled in Eurasia (e.g. the migratory wave scenario, the brain expansion scenario, and the common African home scenario, and the cultural exclusion scenario) [36].

As regards the species responsible for the first diffusion out-of-Africa, an increasing amount of data point out that these hominins were closer to the *Homo habilis* than to *Homo ergaster*. Indeed, the archaic cranial and postcranial features of the earliest known hominin remains, found outside Africa at the

Dmanisi site in Georgia [37], suggest that these hominins were not derived, encephalised, large-bodied, technologically advanced humans with locomotive adaptations to life on the savannah, but were more archaic hominins, perhaps still adapted to life in a woodland landscapes [38-39]. The anatomical features of Dmanissi hominins apparently contrast with the palaeonvironmental context, as inferred by small mammal association found at the site [36], and by palaeobotanical data [40], which depicts an environment dominated by warm steppe, in a context of general aridity. Accordingly, and taking into account that the stratigraphically lowest and highest occurrences of the remains of a species (stratigraphical datum), within a given geographical area, do not necessarily correspond to its actual first/last appearances (palaeobiological events) in time [41], the first appearance of a representative of our own genus out of Africa would have predated the lowest occurrences of its fossil remains at Dmanissi.

Following Agusti and Lordkipanidze [42], the expansion of hominins from East Africa to the southern Caucasus (maybe following a corridor of river systems which seems to have connected Central Africa with the Mediterranean since the Late Neogene [43-44]) would have occurred during any of the interglacial periods in the interval between 2.4 Ma and 1.9 Ma, when pollen data indicate that woodlands extended across the Levant, the Levantine corridor being among the most plausible route for hominin dispersal out of Africa.

Several lines of reasoning, indeed, stress the suitability of coastal environments for “out of Africa” dispersal. Moving along coastlines, hominins could have found relatively abundant nutritional resources [45-46], as well as proper places for at least temporary settlements [47]. Conversely, a dispersal route crossing the south Red Sea at Bab el-Mandeb Straits [48-50] and then crossing the inland regions of the Arabian Peninsula, though practicable during temperate or interglacial stages, seems not to have been easy due to the presence of ecological and physiographical barriers such as deserts, mountain ranges, and large rivers [45,51]. Moreover, these routes would have implied some ability to cross water [52]. Finally, there is no convincing evidence to support the hypothesis of a dispersal route across the Straits of Gibraltar, neither for hominins nor for mammals [53].

Assuming the Levantine corridor route was the most suitable for the dispersal of early honinins towards Eurasia, new questions arise: how many hominin species negotiated such a territory in the Early Pleistocene and how many times did they do it? Did hominins move in multi-species dispersal waves together with the few African mammal species that entered Eurasia?

As regards the dispersal of the first archaic *Homo*, no compelling evidence exists that these hominins moved in concert towards Eurasia with other African mammals. Indeed, the significance of the dispersal of African bovids into Asia at about 2.5 Ma has to be reconsidered [54]and, most importantly, the local faunal assemblages (LFA) of Dmanissi do not seem to support a “migratory wave hypothesis”. The LFA shows marked European affinities and no taxa, among those claimed to have dispersed, roughly coincidentally, into Eurasia around the transition from Gelasian to ‘Calabrian’ (from the first to the second part of the Early Pleistocene as recently redefined, [18,36,55]) have confidently been recorded.

The less advanced hominins of the *H. ergaster*-*H. erectus* group [*H. ergaster* mostly refers to African remains,[56]while *H. erectus* refers to Far Eastern Asia][57-58] first appeared in Eurasia at the beginning of the ‘Calabrian’. Due to doubts about the actual taxonomical status of Chinese hominin remains from Yuanmou [59], the earliest sound evidence for *H. erectus* in Asia comes from deposits at the top of the Sangiran Formation in Java, dated at about 1.6 Ma. However, ancestors of Java hominins might have been present in Asia earlier, as they possibly entered Java during the marked sea lowering between about 1.8 and 1.74 Ma [60], even if the “Stepping Out model” supports a migration around 1.5 [61]. During the drier periods recorded in the Early ‘Calabrian’, the Java environment, with its heterogeneous vegetation, may have supported a diversified fauna, and provided suitable conditions for both fauna and hominin [60]. But, again, the uncertainty as to the actual age of the hominin dispersal makes it difficult to ascertain whether other species dispersed from Africa at the same time, although at least *Pachicrocuta brevirostris* is recorded in Asia around 1.7 Ma.

The arrival in Asia of the ancestor of Java’s hominins looks slightly older than the earliest evidence from Southwestern Asia, where human remains, tentatively attributed to *H. ergaster* or *H. erectus* have been reported from the ’Ubeidiya site (Israel) [62]. Some cranial fragments and teeth have been retrieved as surface finds, while an incisor was found in stratum I-26a of the ‘Ubeidiya Formation, whose fossil-bearing strata has been dated to ca. 1.6 -1.2 Ma [63]. Although the ‘Ubeidiya LFA shows clear European affinities, it counts a number of indisputably African taxa, such as Cercopithecidae (cf. *Theropithecus*), *Crocuta crocuta*, *Megantereon whitei*, *Kolpochoerus olduvaiensis*, *Hippopotamus* and *“Pelorovis” oldwayensis* that suggest that some other mammals could have been involved in the hominin dispersal towards Southwestern Asia. Nevertheless, Bar-Yosef and Belmaker [63], reviewing vegetation and faunal data from key Early and Middle Pleistocene sites of southwestern Asia, stated that, the “incomplete chrono-stratigraphy of this vast region does not allow us to accept the direct chronological correlation between the available sites and the events of faunal and hominin dispersals from Africa”. The same authors proposed that “there is no correlation between hominins and faunal dispersals” and suggested that “early *Homo* dispersals were not directly controlled by climatic forcing”.

The Western Mediterranean scenario

The oldest hominin record in Western Europe is the mandible from the Sima del Elefante (Atapuerca, Spain) dated to about 1.2 Ma [64], but nowadays, there is general consensus in assuming that humans dispersed towards Western Europe during the Early ‘Calabrian’, as demonstrated by archaeological evidence in Spain and possibly in southern France and Italy[65-67].

The first dispersal of some hominin groups towards and across the Mediterranean region, was likely part of a progressive faunal renewal which started during the latest Gelasian and developed by scattered bioevents during the ‘Calabrian’, also involving some large mammals of African origin. This hominin dispersal possibly occurred during a time of environmental instability, when more flexible, opportunistic and omnivorous ‘‘predators’’, such as hominins would have had more opportunities to exploit a broader spectrum of resources than the more specialized species [29]. An important role in the successful human dispersal, was probably played by functional changes which, at the time, characterized the Western Mediterranean palaeocommunities, such as the increasing availability of prey and the abundance of open environment dwellers. But, the presence of large carnivores probably would have reduced the success of the very first, pioneer colonizers of Europe [29].

A few remarks and a research agenda

The increase in environmental variability and periods of changing habitat mosaics undoubtedly could have been among the factors shaping hominin evolutionary patterns, including behavioural flexibility and cultural complexity [68]. The idea that increasing environmental variability, rather than grassland expansion in increasingly arid conditions, might have promoted new survival strategies is supported, for instance, by data on faunal renewal and hominin and lithic artifact appearances in the Turkana Basin [69], as well as by studies on short-term environmental responses to climate variation, locally amplified by high-amplitude tectonic processes such as the development of the Cenozoic East African Rift System [70-71]. On the other hand, a rapid increase in savannah grassland between 1.78 and 1.69 Ma might be consistent with an “adaptive link between the appearance of African *Homo erectus* and the increasingly savannah-dominated environment” [72]. Possibly, grassland expansion had some role in augmenting the complexity and heterogeneity in the variety of environments the early hominins faced [69].

On the other hand, following the “The Out of Africa Technological Hypothesis”, the role played in the hominin’s ability to exploit a range of varying habitats through their peculiar adaptive strategies, behavioural flexibility, cultural complexity and technology cannot be underestimated [15,33,73] .

All in all, as knowledge increases, it has become evident that, although global climatic fluctuations had some effect on the hominin evolutionary process, it was not only climate which shaped the evolutionary history of our own genus and affected hominin behaviour and dispersal. Hitherto available data and several lines of reasoning suggest that some complex, and not always direct, relationships existed between environmental changes and human dispersal and setting. Humans were a generalist species, having broad niches, and were able to negotiate and survive in a variety of environments, beyond their subtropical and tropical African homeland. Early Pleistocene alternating climatic stimuli seem to have only indirectly affected their evolution by promoting changes in the structure of ungulate communities, and, in turn, in the carnivore guild. Moreover, an increasing amount of evidence suggests that hominin movements cannot always be placed in the context of the wider mammalian fauna dispersals, because the more LFAs are found the more it becomes evident that species did not generally move in multi-species dispersal waves, enlarging individually, displacing or contracting their range as the environmental conditions were suitable/unsuitable for them.

To conclude, although during the last couple of decades, important insights have revealed the dynamic nature of climate and the complex responses of species, populations and communities to climate stimuli, and although the hominin fossil record has notably increased and our knowledge of the human dispersals out of Africa has been refined, the chronology and causes behind the original diffusion of hominins “out of Africa” and other more hypothetical dispersals toward and/or within Eurasia is still one of the hottest topics in palaeoanthropology, albeit it remains rather obscure in many respects. Despite the growing amount of data, we are still far from an exhaustive scenario depicting the multifaceted relationships between fauna, vegetation, and humans during the latest Cenozoic.

With the challenging goal of investigating the reliability of hypotheses on the relationships between human dispersal and ecosystem dynamics and constraints, we have to confront, through a more integrated approach, a more comprehensive understanding of their underlying, causal forces and their complex interplay. The reconstruction of the evolution of past paleoenvironments and of the action of single biotic and non-biotic factors on the surroundings and on the structure of land paleocommunities, is a challenging study which requires the cultural and methodological support of disciplines of apparently remote, specialized sectors, such as geochemistry, sedimentology, paleontology, paleoecology, palaeonthropology, palinology and paleobiology. It requires the examination of a large number of variables, as well as of the mutual interchange of results between the various collaborating disciplines as well as the cross-checking of reciprocal inferences. But, since all hypotheses about the environmental effects on evolution depend on temporal correlation, the central challenges are: to finely resolve the chronological framework, to understand the nature of diachroneity among bioevents across geographical and ecological boundaries, to be able to make correlations between distant sequences, as well as to remove the sometimes confusing taxonomical treatments of some species, to improve our understanding of the ecological settings where hominins evolved through advanced palaeoecological approaches, including both classic ecomorphological analysis and new biological and chemical techniques, and to provide high-resolution and integration of discontinuous climatic data, developing a large, multidisciplinary database.

We are optimistic that a broad debate devoted to discussing climate and ecosystem dynamics in the context of human evolution, behaviour and dispersals could stimulate new and more integrated research on these fundamental and fascinating issues.

最近，可能引发非洲古人类进化转折的环境因素正被大量研究。至少在东非，这些环境因素大致支持这样一个典型的模式，即：250万年前，随着气候的变化，植被明显减少，大片的热带草原延伸向低地，原来高海拔处的植物也出现在了低海拔处 [11]。天文因素可引起较短时间尺度的生态系统的波动，局部地区以至整块大陆的地理因素也可能对植被分布有不同影响，研究者们还把目光聚焦到了这两方面上。生存环境多样性导致的复杂模式可能代表了一个早期人类进化时所处的高度变化的时空环境背景[12-16]。土层中碳酸盐和有蹄类动物牙釉质的同位素分析结果，确认了更新世早期东非是以草原为主的生态系统，且在200万年前，早期人类已经可以从空旷的草原至水边森林等这一系列的环境下取得生存资源[17]。尽管在最近几十年里，我们对非洲早期人类起源和进化所处的环境背景有了清晰的认识，但在某些事件中气候所扮演的真正角色却还需讨论，包括驱使人类从非洲向欧亚大陆的扩散，以及非洲其他生物为何没有随迁徙浪潮而走出非洲[18-19]。

气候在促进动物区系进化及功能转移上的作用确实是一个古生物学和古生态学的研究热点。其挑战性在于去明确环境因素在大小动物包括人类的迁徙中的作用。哺乳动物区系的复杂组成(多样性的波动、生物量和古群落的生态结构)中的一些进步性的改变是否可单单归因于气候变化[20-24]，还是由于固有的生物因素在其中发挥重要控制作用，一直以来这都是生态学家和进化学家的分歧之处[25-27]。当然，气候波动和动物区系改变之间的因果关系可能是不同物种各自适应反应累积的结果，这结果可能会影响群体内部动态变化。更进一步，气候变化可能会移除关键物种，造成物种之间关系改变以

及导致生态系统重建 (“共进化不平衡理论”)[28]。 这样看来，气候(例如：全球气候系统在约260万年和100万年前的变化)是引发动物区系重建的关键因素，但是固有的生物因素(竞争/共同进化)影响了动物区系的时间测定及后续结构重建的内容(这与天文因素引起的气候改变并无很大关系)，同时也可能是决定动物区系进化所必需的。

在中纬度地区，通常情况下哺乳动物应对气候变化不只是简单地通过进化、产生新物种或灭绝，还可根据植被覆盖范围和跨纬度的生物群落替换来改变它们的分布范围，这就使得不同物种因应对环境扰动而有不同的扩散 [29]。总之，气候变化通过迁徙和扩散事件，使得多样性增加，但是改变了古生物群落的平衡，导致了动物区系的种类组成和生态结构发生了新的内外动态变化和进步性的演替。内部的动态变化和竞争关系中的改变也可能在动物种群进化中发挥重要作用[29,30]。

但气候对更新世人类扩散及成功迁居欧亚大陆(特别是欧洲西部)有何影响？是什么促进了这些扩散？人类是与其他哺乳类一起扩散的吗？

尽管最近学术界对此的研讨兴趣越发浓厚，解释“出非洲”扩散的时间和方式的不同模型不断被提出[31-35]，一些观点指出需要把“什么人，什么时间，什么地点，为什么，怎么样”等弄清楚后，我们才能自信地回答有关更新世的气候和环境改变对人类在非洲和欧亚之间的迁徙是否有特殊的作用。

新的数据，一方面使我们能够回答诸如“什么人”最先从非洲走向欧亚以及他们可能选择了什么样的路线；另一方面，它让我们质疑之前提出的早期人类为什么走出非洲移居欧亚的模型(例如，迁徙浪潮假说、脑容量增大假说、非洲共同家园假说和文化排斥假说等) [36]。

当讨论到哪个人种最早从非洲迁徙出来的时候，不断增加的数据指出这些早期人类更接近于能人而不是匠人。确实如此，在非洲之外的格鲁吉亚德曼尼西遗址出土了约180万年前的古人类遗骸[37]，他们古老的头盖骨和一些颅后特征显示他们并不是脑容量大、体型大、掌握先进技术而能灵活适应大草原生活的直立人的后代，而是更古老的，或许仍适应森林生活的古人种[38-39]。德曼尼西人的解剖学特征与古环境背景形成鲜明对比，同一遗址发现的小型哺乳动物[36]及古植物学数据 [40]都显示当时该地区是干旱大环境下的温性草原。照此来看，当考虑到在一个给定的地理区域内，按照地层学给出的一个物种的遗迹所处地层的上下关系(地层学数据)其实并不一定与该物种实际出现的先后顺利(古生物事件)一致[41]，那么最早走出非洲的我们人类的代表化石遗迹可能在德曼尼西地层中由最底层转到了上面。

按照 Agusti 和 Lordkipanidze[42] 的观点，早期人类从东非向南部高加索的扩散(可能自新第三纪晚期开始沿着连接中非和地中海的河流走廊迁徙- 参考[43-44])可能发生在190万年至240万年间的任一间冰期，花粉数据显示那时森林地带延伸至黎凡特，那么黎凡特走廊是当时早期人类出非洲迁徙的最合理的路线之一。

这个推理方式确实强调了海边环境适合人类的出非洲扩散。沿海岸线迁徙，早期人类可以有相对丰富的食物来源[45-46]和至少适合暂居的地方[47]。反过来看，经过巴布厄耳曼德海峡穿越红海[48-50]，再穿过阿拉伯半岛的迁徙路线，虽然在气候温和时期或间冰期是行得通的，但在沙漠、高山和大河这些生态和地形障碍面前却是非常不易的[45,51]。另外，这些路线暗示了早期人类具有一些涉水的本领 [52]，最后，没有任何证据来支持早期人类或其他哺乳动物穿过直布罗陀海峡迁徙的假说[53]。

假设黎凡特走廊是早期人类出非洲向欧亚扩散的最佳路线，那么新的问题又出现了：更新世时有多少早期人种走过这片土地，他们走了几次？人类是在多物种迁徙浪潮中与非洲的其他哺乳动物一起走进欧亚大陆的吗？

说到最古老的人类的扩散，其实没有令人信服的证据来说明这些早期人类是与非洲的其他哺乳动物一起走向欧亚的。实际上，250万年前非洲牛科动物向亚洲扩散的重要性还有待于重新定位[54]，更重要的是，德曼尼斯遗址的动物群(LFA)并不支持“迁徙浪潮假说”。该动物群与欧洲的有显著相似性，没有分类，包含在那些大约在格拉斯-卡拉布里亚的转折期由于巧合而被认定进入欧亚的动物群里(最近将时间从更新世早期的第一阶段转至第二阶段)[18,36,55]。

匠人和直立人这些稍低级的早期人类在卡拉布里亚早期最先在欧亚出现[匠人主要指非洲发现的遗迹[56]而直立人主要指远东亚地区[57-58]。鉴于自云南元谋出土的中国的早期人类化石的真正分类学地位难以确定[59]，亚洲最早的直立人的证据来自于距今160万年的爪哇桑吉兰遗址的上层沉积物。

然而，爪哇猿人的祖先却可能早已在亚洲出现，他们很可能在174-180 万年前海平面显著降低的时候来到爪哇 [60]，尽管“走出去模式”支持约150万年前的迁徙[61]。在卡拉布里亚早期的干旱阶段，爪哇可能以其不同的植被养活了一个多样的动物群，为动物和早期人类提供了适宜的生存环境[60]。但是，早期人类扩散时间的不确定性又使得有无其他物种同时出非洲的问题变得难以回答，但至少在亚洲发现了距今约170万年的短吻硕鬣狗。

亚洲西南以色列尤贝蒂雅遗址的古人种近于匠人和直立人，但到达亚洲的爪哇猿人的祖先看上去还要古老一些[62]。在尤贝蒂雅遗址的表层发现了一些头盖骨碎片和牙齿，在 I-26a岩层中则发现一颗门牙，该处有化石的地层可追溯至120-160万年前[63]。尽管尤贝蒂雅的动物群明显与欧洲的有着较近的亲缘关系，但它里面还是有一些毋庸置疑的非洲种类，例如狝猴亚科(狮尾狒属)、斑鬣狗、巨颏虎、非洲野猪、河马和长角牛等，这表明其他一些哺乳动物也随人类迁徙到了亚洲西南部。尽管如此，Bar-Yosef 和 Belmaker 2010年[63]又对亚洲西部更新世早期和中期的关键遗址的植被和动物群进行了分析，表达了如下观点：这个广阔地区的年代地层学资料是不完整的，资料的欠缺阻碍了我们去认可已有的遗址与动物群和人类出非洲事件在时间先后顺序上的关联性。这两位学者还认为“早期人类和动物群这两者的扩散并没有联系”，并表示“早期人类的扩散并不直接被气候左右”。

欧洲西部最古老的人类化石是西班牙阿塔坡卡的埃勒芬特裂谷洞穴所发现距今约120万年的下颚骨[64]，但现在，大家普遍认同人类向西欧的迁徙是在卡拉布里亚早期，这被西班牙和意大利的考古学证据所支持[65-67]。

一些人类种群向地中海地区最早的迁徙可能是进步性的动物区系重构的一部分，该重构自格拉斯晚期开始，在卡拉布里亚时期经分散的生物事件而得到发展，这其中也包含了非洲起源的一些大型哺乳动物。这一次的人类扩散可能发生在自然环境不稳定的时期，更灵活、投机和杂食性的“捕食者”，比如人类，将比食性更专一的物种有更多的机会去开辟更广阔的捕食空间[29]。功能性改变在这次人类成功扩散中很可能起着重要作用，这改变了当时地中海西部地区古群落的特征，比如不断增加的猎物以及生活在开放环境里的数量丰富的动物等。但是，大型的食肉动物的存在很可能降低了人类最早到欧洲的开拓性迁居的成功率[29]。

环境多样性的增加以及栖息地交替演变的时期，毫无疑问是影响人类进化模式的因素，包含行为灵活性和文化复杂性 [68]。环境多样性的增加而不是持续干旱条件下草原的扩张可能造成了新的生存策略，该假说有图尔卡纳盆地的动物群系重构以及人类和石制品的特征等数据所支持[69]；短期的环境对气候多样性的反应研究，例如新生代东非大裂谷这样的局部地区地理大重构等也支持该假说[70-71]。另一方面，169-178万年间热带大草原面积的快速增长可能与“非洲直立人的出现和逐渐被热带草原主宰的环境之间的适应性环节”是一致的 [72]。草原的扩张可能在增加早期人类所面对的多样环境的复杂性和异质性上起作用[69]。

从另一个角度来看，按照“出非洲技术假说”，人类通过自己特有的适应策略、行为弹性、文化复杂性和技术等去开拓不断变化的生境的能力没有被低估 [15,33,73]。

总之，随着相关知识的不断丰富，我们已经清楚地认识到尽管全球气候波动对人类进化过程有一些影响，但不仅仅是气候决定了我们人类的进化历史并影响了人类的行为和扩散。现有的数据和推理表明环境变化和人类扩散与定居之间存在一些并不总是直接的而是复杂的关联。人类是一个广食性物种，有大的生态位，离开了他们亚热带和热带的非洲故乡而能够在多样性环境下适应和生存。更新世早期的不断交互的气候刺激改变了有蹄类动物群体的结构，同时也给食肉动物种团带来了些许变化，以此来间接地影响人类的进化。更进一步地说，不断增加的证据显示人类迁徙不能总放到野生哺乳动物群扩散的大背景下考虑，因为考古学上越多的动物群被发现，就越清楚地知道各物种并不是在多物种扩散浪潮中一起迁徙的，而是根据环境条件是否适合来替换或缩减各自的分布范围。

总起来说，尽管在过去几十年里，许多重要发现已揭示了气候的动态属性以及各物种、群体和群落对气候刺激的复杂反应，尽管随着出土的人类化石越来越多，我们对于人类出非洲扩散有了新的认识，但人类最早出非洲扩散的年代及原因和其他假设的人类向欧亚或在其内部的扩散仍是古人类学研究的热点，虽然其对很多问题的回答还是模糊的。尽管数据越来越多，我们仍对新生代动物群、植被和人类间多方面的联系难以有一个详尽的解释。

人类扩散和生态系统的动态变化与环境制约之间的关系的假说是否可信，带着这个颇具挑战性的目标，我们需要从一个更综合的角度，去对它们隐含的因果力及其复杂相互作用有一个更充分的理解。重建古生境演化和单一生物因素和非生物因素对陆生古群落结构及其周围环境的作用，是一项有挑战性的研究，这需要在文化和方法学上对地球化学、沉积学、古人类学、古生物学和古生态学等多学科的看似不相关的知识进行整合。它需要对一大批的变量以及各合作学科间相互交换的结果做检查，还需对各自的推论做重复检验。但是，因为所有关于环境对进化影响的假说都是基于时间上的相关性，则关键问题在于：能很好地解决时间框架问题；能理解跨越地理和生态界限的生物事件的穿时性；能够去建立久远事件间的相互联系并将一些物种的含糊分类剔除；通过高级的原生态途径去提高我们对人类进化所处的古生态环境的理解，这些途径包括传统的生态形态学分析和新的生物和化学技术研究等；能够提供高分辨率、高度整合的不连续气候数据，建立一个大的多学科交互的数据库。

这次广泛的研讨致力于在人类进化、行为和扩散的背景下，讨论气候和生态系统的动态变化，它将会在这些基本的、有趣的问题上促进新的更完善的研究工作的开展，这也是我们期待的。(王传超 译)

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