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The behavioural ecology of hominin locomotion: what can we learn from landscapes of fear and primate terrestriality?

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A defining feature of the hominin clade is bipedality, often parcelled together with terrestriality. However, there is increasing evidence of locomotor diversity, both within the hominin clade and amongst the Miocene apes that came before them. There is also growing recognition that bipedalism might have arboreal origins and that arboreality persisted in several hominin taxa, including our own genus *Homo*. Furthermore, the difference between terms like “habitual” and “obligate” bipedality is not clearly defined and is often inferred from fossil features, rather than a description of each behaviour *in vivo*. Combining fossil and palaeoecological evidence with insights from behavioural ecology facilitates new interpretations of evolutionary pathways and highlights the importance of considering convergent evolution in the emergence of locomotor traits and characteristics. Taking such an approach also moves away from assumptions of a straight-line trajectory towards modern human locomotion and explores the likelihood that independent forms of bipedality and terrestriality arose at different times and in different combinations with other features of ape morphology and behaviour. Evidence from extant primate species can broaden our understanding of the correlates, causes, and consequences of terrestriality and can be used to generate hypotheses which are then explored further using paleontological methods. In this paper, we explore the evolutionary origins of hominin locomotion, but extend our review to include broader timescales, a wider range of primate taxa, and an integrated set of methods and disciplines for generating and testing hypotheses about locomotion. Perceived risk (or, the “landscape of fear”) is a key pressure that has selected for primate arboreality – particularly nocturnal arboreality. We propose that shifts in Plio-Pleistocene landscapes of fear – caused by declining carnivore abundance and diversity – might also have been a key selection pressure in changes to primate locomotion, particularly papionin and hominid terrestriality. We discuss this hypothesis and propose future research avenues to explore it further. Not only will such research provide a more nuanced view of the causes and consequences of a rare behavioural trait in primates, but it could ultimately help us explain how one group of African apes came to spend all their time on the ground, and how that made them human.

KEYWORDS

hominin evolution, bipedalism, primate terrestriality, papionin behaviour, predator-prey dynamics, landscapes of fear, behavioural ecology

1 Introduction

Philosophers and scientists have long tried to pinpoint just what makes humans a “uniquely unique species” (Alexander, 1990). Whether or not it is valid – or morally appropriate – to distinguish humans from all other animals in this way, especially with an assumption of human superiority (Chapman and Huffman, 2018), it is still fascinating to consider the traits that define us as a species. Such traits have been explored both by delving into the past through paleoanthropology, and by analysing modern human behaviour. In the paleoanthropological world, fossils are classified as hominins i.e., more closely related to humans than to chimpanzees, based on two key morphological traits; (1) reduced canine size with loss of canine honing complex, and (2) indicators of bipedal locomotion (Almécija et al., 2021; Harcourt-Smith, 2010). When modern humans are compared to other animals, it has been argued that our cognition, cooperation, culture and/or social structure set us apart (DeVore and Tooby, 1987; Foley and Gamble, 2009; Hill et al., 2009; Tomasello and Vaish, 2013). However, the evolution of these complex adaptations is attributed to a set of key “pre-adaptations” that include the emergence of bipedalism facilitating broader dispersal, social changes, and manual dexterity, and therefore a dietary shift towards hunting and extractive foraging. It has been hypothesised that this change in diet coevolved with provisioning and task specialisation, along with cognitive skills like imitation and shared intentionality which underlie human culture and cooperation (Hill et al., 2009).

Thus, whilst paleoanthropologists focus on the morphofunctional indicators of bipedality and evolutionary anthropologists perhaps more on the behavioural aspects of bipedalism, they appear to agree that walking upright on two legs is fundamental to what makes us human. Built into this understanding is that hominin bipedality is a terrestrial mode of locomotion, making modern humans the only primate species to live almost exclusively on the ground. However, it is possible that bipedality and terrestriality emerged at different times and under separate selection pressures (Richmond et al., 2001; Takemoto, 2004), and it is therefore important to explore and understand the roots of both behaviours separately. Additionally, given that both bipedality and terrestriality are rare amongst primates, we should examine their emergence and drivers not only within our own lineage, but also where they are evident across other extant and extinct genera. For example, studies of orangutan locomotion are expanding our set of hypotheses about hominin bipedality to include an arboreal origin (Crompton et al., 2010a; Thorpe et al., 2007). And our study of hominin terrestriality should be informed by evidence collected across extant and extinct members of the Papionini tribe, which contains the highest concentration of terrestrial primate taxa (Estrada and Marshall, 2024).

Not only should we broaden the taxonomic context in which we explore the evolution of bipedality and terrestriality, but also our investigative methods. In this paper, we discuss how combining fossil and palaeoecological evidence with insights from behavioural ecology can facilitate new interpretations of evolutionary pathways and bring in nuanced considerations, such as the role of homoplasy

as well as homology in the emergence of locomotor characteristics. A more integrated and interdisciplinary approach can also help shift false assumptions about a straight-line trajectory towards modern human locomotion. Instead, it can be used to explore the likelihood that independent forms of bipedality and terrestriality arose at different times and in combination with different features of primate locomotion. The approach can thus be used to examine terrestriality across pockets of the Hominini and Papionini tribes – both extant and extinct – which might provide clues about the ecological drivers of this rare trait in primates, giving us a window into the origins of human locomotion. Through an iterative process, morphological and behavioural evidence from extant primate species can broaden our understanding of the correlates, causes, and consequences of increased terrestriality, both to test theories about the origins of locomotor characteristics, and also to generate hypotheses that can then be tested and refined further using paleontological methods.

In Section 2, we review paleontological evidence for the evolution of hominid and hominin locomotion, recognising that we need to look further back than the emergence of “obligate bipedalism” sometime in the Plio-Pleistocene to examine the primates and paleoenvironments of the Miocene. In Section 3, we highlight that the range of terms describing bipedality – “habitual”, “committed”, “obligate” – are not clearly defined and are often used to describe different fossil features rather than different *in vivo* behaviours. This emphasizes the importance of integrating fossil evidence with paleoecological evidence and insights from behavioural ecology. We review evidence on the evolution of primate terrestriality more broadly, along with discussion about traits that are associated with more time spent on the ground. These range from morphological features like larger bodies to complex behavioural traits like tool-use. In Section 4, we highlight that a behavioural ecology lens can enhance our understanding of some of the more dynamic aspects of paleo-environments, such as predator-prey interactions and the effects of “landscapes of fear” on primate behaviours. We summarise evidence from extant primates showing a negative relationship between perception of risk in the environment and time spent on the ground, and discuss the potential effects of this relationship on primates’ social and cognitive capacities. We then return to the fossil record to assess hypothetical Plio-Pleistocene “landscapes of fear” in terms of the broad trends seen in the hominin, carnivoran, paleoenvironmental, and archaeological records of eastern and southern Africa. We highlight the inherent difficulties of working with data representative of vast spatiotemporal scales, but outline some of the insights that can be gleaned from the fossil record about the behaviour of primates and carnivores throughout evolutionary history. Figure 1 summarises the broad paleoclimatic, paleoecological, paleontological and archaeological trends reviewed in this paper.

Through this paper, we demonstrate that behavioural ecology evidence indicates that the landscape of fear might have been a key selection pressure shaping primate locomotion. Rather than assuming that the shared characteristic of terrestrial behaviour amongst extant African apes was inherited directly from their last

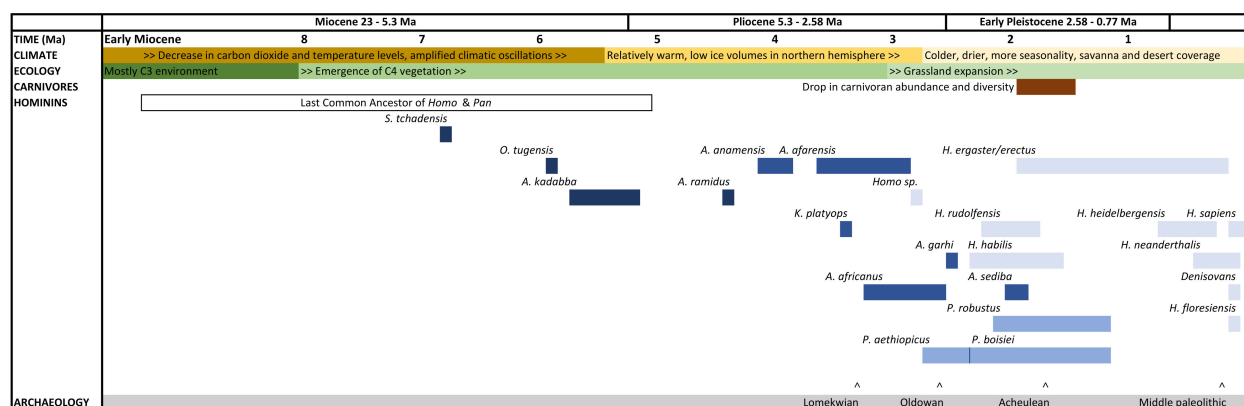


FIGURE 1

A timeline of African hominin evolution alongside ecological and archaeological trends and the hypothesised drop in carnivore abundance and diversity.

common ancestor, we propose that the dramatic loss in carnivore abundance and diversity over the past three million years has allowed all African apes, as well as many papionins, to become more terrestrial than their ancestors, albeit with different styles of locomotion. We propose integrated methods and particular fossil sites and time periods that could broaden our understanding of how localised fluctuations in predator abundance or diversity might have facilitated the rise of terrestriality in certain primate lineages. Not only will this provide a more nuanced view of the causes and consequences of a rare behavioural trait in primates, but it could also help explain how one group of African apes came to spend all their time on the ground, and how that made them human.

2 The evolution of hominin locomotion

As stated above, bipedal morphology is one of the defining features of the hominin clade, emerging after we shared a last common ancestor (LCA) with chimpanzees and bonobos, between 10 and 6 million years ago (Ma) (Moorjani et al., 2016; Prado-Martinez et al., 2013; Wilkinson et al., 2011). For many years, prevailing questions were thus about when and why hominins “stood up” from all-fours to walk on two legs, under the assumption that characteristics like quadrupedalism and knuckle-walking – which are shared amongst non-human African great apes – were present in our LCA (Richmond et al., 2001). However, the reliance on studies of extant great apes to deduce LCA morphology and behaviour often assumes that their modern-day similarities are examples of homology (shared ancestry) rather than homoplasy (convergent evolution due to similar environmental pressures). It also assumes that modern apes inhabit environments so similar to those of the LCA that they have not faced new selection pressures resulting in significant evolutionary change since the LCA (Sayers et al., 2012). Contrary to such assumptions, there is evidence that variation in hand and wrist morphologies of modern apes is more suggestive of *independent evolution* of knuckle-walking in the *Pan*

and *Gorilla* lineages (Dainton and Macho, 1999; Kivell and Schmitt, 2009). To get a fuller picture, these top-down explorations of ape evolution must therefore be complemented by bottom-up explorations of the ape fossil record (Almécija et al., 2021; Lovejoy et al., 2009b).

2.1 Miocene apes and the origins of hominid locomotion

The Miocene (~23 – 5.3 Ma) has been dubbed “the real planet of the apes” (Begun, 2015) and is therefore a critical period for exploring the deep roots of locomotion in hominoids (all apes), hominids (the great apes), and hominins (the human lineage) (Almécija et al., 2021; Urciuoli and Alba, 2023). Unfortunately, the African ape record is sparse between ~14 and 10 Ma but rare exceptions, such as the discovery of an infant ape cranium in Kenya, *Nyanzapithecus alesi* (~13 Ma), provide insights into potential stem hominoids. *Nyanzapithecines* share similarities with extant hylobatids (gibbons) with their relatively small bodies and arboreality, but the inner ear of the *N. alesi* cranium suggests that their movements were probably less acrobatic than modern-day gibbons (Nengo et al., 2017).

Ongoing debate about where and when the earliest hominids emerged will likely remain unresolved whilst this critical gap in the African fossil record persists. One possibility is an “out of Africa” and then “back-to-Africa” sequence of events, with aridification of the Sahara creating a biogeographic barrier between African and southern European faunas (Bibi, 2011; Schuster et al., 2006, 2009). The first fossil evidence of apes outside of Africa comes from Europe in the middle Miocene (~16.5–14 Ma) and many of the most recent Miocene apes for which we have postcranial remains have been found in Europe. These include *Pierolapithecus catalaunicus* (~11.9 Ma) (A. S. Hammond et al., 2013; McNutt et al., 2018; Moyà-Solà et al., 2004), *Danuvius guggenmosi* (~11.6 Ma) (Böhme et al., 2019a), and *Rudapithecus hungaricus* (~10 Ma) (Begun et al., 2012; Ward et al., 2019).

The foot, hand, and pelvic morphologies of *Pierolapithecus* suggest that it lived a fully arboreal lifestyle, did not engage in suspensory locomotion, and was more frequently engaged in orthograde (upright body posture) behaviours than earlier hominoids, but not as frequently as extant great apes (Hammond et al., 2013; Moyà-Solà et al., 2004). In contrast, *Rudapithecus* and *Danuvius* show adaptations to suspensory locomotion and there has even been an argument for evidence of above-branch bipedalism in the latter (Böhme et al., 2019a; Ward et al., 2019), although this is contested (Williams et al., 2020).

These Miocene apes from Europe provide a diverse set of possibilities for the roots of hominid locomotion, but the three genera described above share characteristics that could have been present in the LCA of African hominids. For example, at ~30kg in body mass, these apes were all smaller than extant great apes (perhaps with the exception of bonobos) [*Pierolapithecus*: (Moyà-Solà et al., 2004); *Rudapithecus*: (Smith et al., 2019); *Danuvius*: (Böhme et al., 2019b)]. They show adaptations to an arboreal lifestyle and indicate early origins of an orthograde body plan that could then have been co-opted for behaviours including below-branch suspension, knuckle-walking, and/or arboreal or terrestrial bipedalism in different hominid taxa. Emergence of this upright posture is documented alongside an increase in ape brain size – both examples of traits that are central to discussions about human evolution but are in fact rooted in evolutionary trends seen as far back as the Miocene (Alba, 2010; Almécija et al., 2021; Moyà-Solà et al., 2004).

As evidence about the diversity, evolutionary relationships, and geographic dispersals of Miocene apes continues to emerge, albeit mired in controversy (Grabowski and Jungers, 2017; McNulty, 2010; Urciuoli and Alba, 2023), more fossil discoveries will help piece together the connections between ape species from European fossil sites and those found in later Miocene African sites. One such connection has been suggested based on the resemblance between *Nakalipithecus* (9.9 – 9.8 Ma) fossils, found in Kenya, and those of *Ouranopithecus* (9.6–8.7 Ma), found in Greece and a proposed candidate close relative of the extant African great apes (Kunimatsu et al., 2007). Both of these genera, along with *Samburupithecus* (9.5 Ma) (Ishida and Pickford, 1997) and *Chororapithecus* (10 Ma) (Suwa et al., 2007), have been hypothesized as larger-bodied apes, perhaps comparable to extant gorillas. However, most analyses come only from craniodental evidence, except for two isolated phalanges from *Ouranopithecus* which have been used to propose that it might have been “a ground dweller closer to *Papio* and *Macaca* than to *Hylobates* or even to *Pan*” (de Bonis and Koufos, 2014). However, this suggestion is hard to substantiate without further postcranial evidence, and would benefit from an integrated analysis of other ecological drivers that might have driven this locomotor style.

By one analysis, there have been “a series of selective regime shifts” that have influenced ape body size (and locomotion) across the Miocene, shifting from a hominoid LCA that was gibbon-like to a *Pan-Homo* LCA that was chimpanzee-like in size (Grabowski and Jungers, 2017) and – by some arguments – in behaviour (Williams et al., 2023). However, it is difficult to plot out the diverging

evolutionary trajectories of the different hominid taxa, due to the scarcity of fossils from the ancestors of extant African ape clades. Other than a few teeth and a possible proximal femur, we have no fossil evidence for the chimpanzee or gorilla lineages (Cote, 2004; DeSilva et al., 2006; Kunimatsu et al., 2007; McBrearty and Jablonski, 2005; McNulty, 2010; Pickford and Senut, 2004; Suwa et al., 2007). There is fossil evidence of three ape genera from northern and eastern Africa in the late Miocene, all of which have been putatively assigned to the hominin lineage: *Sahelanthropus*, *Orrorin*, and *Ardipithecus*. The traits of these genera are discussed below, with a focus on their inferred styles of locomotion.

At approximately 7 million years old (Lebatard et al., 2008), *Sahelanthropus tchadensis* fossils from Chad represent the oldest putative hominin, initially classified as such based on its dentition and the position of its foramen magnum, perhaps indicative of bipedality (Brunet et al., 2002; Neves et al., 2024; Zollikofer et al., 2005). However, this ape retains many primitive features similar to earlier apes like *Pierolapithecus*, and the foramen magnum positioning may simply indicate orthograde posture rather than necessitating bipedality (Andrews, 2020). Recent discovery and analyses of postcranial material have resulted in varying interpretations of *Sahelanthropus* ranging from habitually bipedal but still engaged in “substantial arboreal behaviour” (Daver et al., 2022), to “not habitually bipedal” (Macchiarelli et al., 2020), and “not an obligate biped, but [...] a Miocene hominid with knuckle-walking adaptations” (Meyer et al., 2023). New fossils, further analyses, and clearer definitions of bipedalism will all be needed to clarify the locomotor style and status of this taxon.

Orrorin tugenensis fossils discovered in Kenya and dated to ~6 Ma have also been given hominin status by some, based largely on an initial proposal that its femur morphology was more similar to modern humans than to other extant apes or *Australopithecus* species, indicating that it was adapted to terrestrial bipedalism of some sort, whilst retaining good climbing adaptations (Senut et al., 2001). More recent interpretations of femoral evidence highlight that *Orrorin* shares many features with earlier Miocene apes and later hominins, and likely represents an “intermediate” morphology between them (Almécija et al., 2013; Richmond and Jungers, 2008).

At the very end of the Miocene (~5.8 – 5.2 Ma) evidence of *Ardipithecus kadabba* from the Middle Awash, Ethiopia, has also been dubbed “the first hominin”, due to the possible absence of a functional canine honing complex, and some indicators of “an early form of terrestrial bipedality” (Haile-Selassie, 2001). However, depending on how morphological comparisons are made, different conclusions can and have been reached about *Ardipithecus*. These range from assigning it the status of the first hominin, to the *Homo-Pan* LCA, to a genus more related to chimpanzees than to the hominin lineage (Haile-Selassie, 2001; Sayers et al., 2012; Senut et al., 2001).

Interpretations relying on assumptions that the LCA was essentially chimpanzee-like use chimpanzee morphology as a reference point to assess how “hominin-like” a fossil is, rather than acknowledging that both later hominins and chimpanzees are likely to display very different, derived features from their LCA. Researchers trying to move away from an over-reliance on this

“Chimpanzee Referential Doctrine” have highlighted that because *Ardipithecus* does not exhibit clear adaptations to below-branch suspension, knuckle-walking, or vertical climbing, it should not be assumed that these styles of locomotion existed in the LCA of *Homo* and *Pan* (Sayers et al., 2012).

2.2 Plio-Pleistocene apes and the origins of hominin locomotion

The Plio-Pleistocene represents a key period for understanding hominin evolution. It encompasses the existence, and even co-existence of at least three hominin genera – *Australopithecus*, *Paranthropus*, and *Homo* – but this diverse clade was pruned down by the disappearance of *Australopithecus* and *Paranthropus* by 1 Ma. Meanwhile, *Homo* appears to have flourished within Africa and in its dispersal out of Africa and across Eurasia ~1.8 Ma (Behrensmeyer, 2006; Potts, 2013; Stringer, 2002; Wood and Boyle, 2016), likely signalling the successful locomotor strategy of a committed terrestrial biped and initiating the subsequent ecological hegemony of *H. sapiens*. The Plio-Pleistocene also marks a period of climatic and ecological change that resulted in the expansion of grasslands across Africa (Cerling et al., 2011; Levin, 2015; Negash et al., 2024). It is this shift towards more open environments that laid the foundations for the “Savannah Hypothesis” – the idea that human bipedality is an adaptation to receding forests (Dart, 1925). This hypothesis gained and retained attention in popular understandings of human evolution and has been closely linked with human tool-use, hunting, and expansion of brain size (Brain, 1981; Dart, 1925, 1949; Darwin, 1871; Harcourt-Smith, 2010; Senut et al., 2018; Vrba et al., 1989; Washburn, 1960). However, several lines of evidence – discussed below – suggest that bipedality was not driven solely by expanding savannahs, and that the relationships between these characteristics and open environments are nuanced.

After appearing in the Miocene, *Ardipithecus* is represented in the Pliocene by the species *Ardipithecus ramidus*, a “primitive” bipedal ape that ranged in wooded habitats in the area now known as the Afar of Ethiopia, ~4.4 Ma (Semaw et al., 2005; White et al., 2009). Initial interpretations of *Ardipithecus* postcranial material posit that this possible hominin combined some form of terrestrial bipedality with arboreal clambering, which involved weight-bearing in the palms and was unlikely to include knuckle-walking. However, this style of locomotion was not well-adapted to long bouts of terrestrial bipedalism, nor to the levels of suspensory arboreal locomotion seen in the African apes of today (White et al., 2009, 2015). Recent analyses of *Ardipithecus* fossils have prompted some researchers to say that it did in fact engage in suspensory locomotion and maybe even knuckle-walking, because its hand morphology is closer to extant apes than more generalised quadruped primates (Prang et al., 2021). A similar argument has been used to propose that its feet were also more similar to those of extant African apes than previously thought (Prang, 2019, 2022). Other researchers do not believe that these similarities warrant the conclusion that *Ardipithecus*’ locomotion was anything like that of

modern African apes, and highlight that comparisons using extant primate data continue to be limited whilst we have almost no fossil record for *Pan* or *Gorilla* (Chaney et al., 2022).

Separating homologous and homoplastic traits amongst extant apes will certainly be made easier through the discovery of more fossils, but it can also be aided by considerations of selection pressures that shaped the behavioural ecology of these lineages. For example, the LCA of all extant African apes is often assumed to have been at least semiterrestrial, because terrestrial behaviour is seen in gorillas, chimpanzees, bonobos, and humans. However, evidence from several Miocene ape fossils (discussed above) suggests they were arboreal creatures, and some interpretations of the *Ardipithecus* evidence indicate that the LCA of *Homo*, *Pan*, and *Gorilla* was probably an above-branch clambering quadruped from whom the extant apes independently acquired their specialisations for suspension, vertical climbing, knuckle-walking, and terrestrial bipedality (Dainton and Macho, 1999; Kivell, 2019; Lovejoy et al., 2009a). We must therefore consider ecological factors that might have selected for increased terrestrial behaviour across all these lineages (convergent evolution), rather than assuming that the shared characteristic necessitates its existence in their LCA.

Whilst debate about the positional behaviour of *Ardipithecus* continues, evidence suggests that it lived in forested habitats and had a C₃-heavy diet. Although not absolute, C₃ and C₄ isotopic signatures have been associated with woodland and grassland vegetation respectively (Cerling et al., 2015). Together, this paleoenvironmental and isotopic evidence indicates that locomotor adaptations seen in *Ardipithecus* fossils were not driven by a move onto the savannah (White et al., 2009). Indeed, the influence of expanding grasslands has more often been linked to the emergence of the genus *Australopithecus* – the first apes considered to be indisputably hominin and referred to as “committed”, “obligate”, or at least “habitual” bipeds (Anaya et al., 2021; Bobe et al., 2020; Harcourt-Smith, 2010; Stamos and Alemseged, 2023; White et al., 2009). However, as this range of descriptors suggests, there is still much debate around the exact nature of locomotion in *Australopithecus* species, and there was probably locomotor diversity within the genus (Senut et al., 2018). At first, *Australopithecus* was contrasted with the “more primitive” *Ardipithecus* to suggest that the derived postcranial features of *Australopithecus* showed that they “had largely abandoned locomotion in the arboreal canopy” (White et al., 2009). However, there is increasing evidence that the morphology, paleoecology, and diet of *Australopithecus* was more adapted to woodland-living than initially thought, especially when the genus first emerged (Bobe et al., 2020; Cerling et al., 2013; Sponheimer et al., 2013).

Au. anamensis first appears in the Kenyan and Ethiopian fossil records from ~4.2 Ma (Ward et al., 1999, 2001; White et al., 2006). Similarities in the paleoecology and faunal records at Kanapoi in the Turkana Basin, Kenya, and Asa Issie in the Afar, Ethiopia, highlight the biogeographic connections that must have existed between these sites, and suggest that *Au. anamensis* thrived in habitats with a mix of C₃ and C₄ vegetation, although they still showed a preference for C₃ foods at this time (Bobe et al., 2020). Their probable

descendants, *Au. afarensis*, were the first hominins to incorporate C₄ foods into their diets ~3.7 Ma, whilst still living in relatively wooded environments (Sponheimer et al., 2013). *Au. afarensis* is probably also the hominin species most associated with early bipedality, famous for both the “Lucy” skeleton and the Laetoli footprints that have been attributed to the species (Kimbel and Deleuzene, 2009; Leakey and Hay, 1979; Raichlen et al., 2008). These footprints are strong evidence that hominins did travel on the ground with a bipedal gait, but the tracks could have been made by a stride very different to modern human locomotion (Raichlen et al., 2008). Recent analyses of additional trackways indicate that there may even have been more than one species of “small, cross-stepping bipedal hominin” traversing the Laetoli landscape over 3.5 Ma (McNutt et al., 2021). If so, this evidence would suggest that the emergence of terrestrial bipedality was not necessarily rare or unique to one species, but an adaptive response by several ape species to shared selection pressures at the time. Indeed, analyses of hominin foot morphologies indicate a diversity at the base of the lineage suggestive of different styles of locomotion and “experimentation in bipedalism” (DeSilva et al., 2019).

Whilst *Australopithecus* is the first hominin genus in which bipedal locomotion is undisputed (Potts, 2013), it does not necessarily mark a transition to exclusive terrestriality, as will be outlined in the sections below. Species of *Australopithecus* disappear from both the eastern and southern African fossil records during the Early Pleistocene; *Au. sediba* from South Africa less than 2 Ma (Dirks et al., 2010), and other members of the genus from eastern and southern Africa ~2.5 Ma (Wood and Boyle, 2016). Evidence shows that *Australopithecus* overlapped both temporally and geographically with two other hominin genera; the megadont, *Paranthropus*, and early species of our own genus, *Homo* (Herries et al., 2020; Jablonski et al., 2008; Potts, 2013; Wood and Boyle, 2016).

Paranthropus appears in the eastern and southern African fossil records ~2.7 Ma and 2 Ma respectively, and disappears from both ~1.2 Ma (Potts, 2013; Wood and Boyle, 2016). Carbon isotope analyses of teeth from *P. boisei*, present in eastern Africa from 2.3 Ma until 1.2 Ma, suggest that the species was a C₄ specialist and indicate that its style of locomotion must have allowed it to exploit open grasslands (Sponheimer et al., 2013). The earliest evidence of the genus *Homo* is a little older, just pre-dating the start of the Pleistocene; one specimen identified as a *Homo* mandible is thought to be ~2.8 million years old (Villmoare et al., 2015). *H. habilis* and *H. rudolfensis*, appear in the fossil record between 2.5 and 2 Ma, and disappear between 1.8 and 1.6 Ma, whilst the first clearly “premodern human”, *H. erectus*, originated at least 1.89 Ma, dispersed across and out of Africa, and only went extinct less than 200 Ka (Hammond et al., 2021; Herries et al., 2020; Rizal et al., 2019; Wood and Collard, 1999).

Compared to the C₄ specialisation indicated by *P. boisei* fossils, *Homo* teeth indicate a mixed diet, composed of both C₃ and C₄ resources (Sponheimer et al., 2013). This suggests that, although *Paranthropus* and *Homo* species were at times sharing relatively small habitats (Bobe and Carvalho, 2019; Hatala et al., 2024) and dealing with the same climatic shifts – increasing aridity, seasonality, and mosaic habitats – they were utilising the

environment differently. It seems that perhaps *Paranthropus* lived and foraged predominantly in the more open C₄ areas, whilst *Homo* inhabited a wider range of environments (Cerling et al., 2013). Both genera appear to have been bipedal, but morphological evidence suggests that this mode of locomotion was less specialised in *Paranthropus* than in *Homo* species (Harcourt-Smith and Aiello, 2004; Richmond et al., 2020).

The brains of *Homo* and *Paranthropus* also display significant differences; the skulls and endocasts of the latter are not distinct from those of *Australopithecus*, and are possibly even less developed, whilst the big size and shape of the *Homo* brain are two of the most distinguishing features of the genus (Falk et al., 2000). This difference suggests that the larger brains observed in *Homo* species cannot be attributed only to environmental shifts, as evidenced by the fact that smaller-brained *Paranthropus* hominins successfully existed through at least a million years of climatically variable Pleistocene, as well as at least half a million years of co-existence with *Homo*. To disentangle assumptions that connect modern human tool-use, hunting, and brain size with a pre-historic move into grasslands, it is thus useful to compare *Homo* records to those of *Paranthropus* and grassland-dwelling papionins, like *Theropithecus*, who were subject to the same selection pressures. Furthermore, as discussed below, the behavioural ecology of the extant *Theropithecus gelada* can complement fossil record interpretations to hypothesise about foraging strategies, substrate-use, and exposure to competition or predation pressure in grasslands.

Despite strong evidence of some form of terrestrial bipedality from as far back as the footprints and derived foot morphology of *Au. afarensis* (Ward et al., 2011), adaptations for and evidence of arboreal locomotion are seen in that species (Kappelman et al., 2016; Senut and Tardieu, 1985; Stern and Susman, 1983; Ward, 2002) as well as in several hominin taxa that both pre and postdate *Au. afarensis*. There has been heated debate about whether such morphological traits are simply a retention of “primitive” ancestral adaptations, no longer in use nor adaptive in hominins, or if they are proof of continued arboreality in multiple hominin genera (Anaya et al., 2021; Kimbel and Deleuzene, 2009; Ward, 2002). Several lines of evidence – including hominin fossils themselves, and the integration of paleoecological data with applied insights from primate behavioural ecology – suggest that these signals should not be dismissed as primitive relics “leftover” from pre-hominin ancestors.

2.3 Signals of arboreality in a range of hominin fossils

From hominin fossils themselves, we see indicators of arboreality in a diversity of taxa. Described above is the postcranial evidence from the eastern African Pliocene species, *Au. anamensis* and *Au. afarensis* (Kimbel and Deleuzene, 2009; Ward, 2002; Ward et al., 2001). Arboreal adaptations are also seen in southern African species of the genus. *Au. africanus* appears in the southern African fossil record ~3 Ma, which is

more recent than the eastern African *Au. afarensis*. Although there is some evidence of reduced arboreality in this species (at least in comparison to extant great apes) (Georgiou et al., 2020), its morphology is generally interpreted as better suited to climbing than the eastern African *Australopithecus* (Green et al., 2007). This interpretation prompts questions about whether climbing adaptations in *Au. africanus* were “secondarily derived” after arboreality declined in the ancestral *Au. afarensis*. Alternatively, both *Au. afarensis* and *Au. africanus* might have inherited their arboreal adaptations from a primitive ancestor. However, if *Homo* is a descendant of *Au. africanus* (as has been proposed), this scenario would suggest that derived terrestrial bipedality evolved independently in the *Au. afarensis* and *Homo* lineages at different times and in different forms (Green et al., 2007; Prabhat et al., 2021). Again, such a scenario suggests that mosaic styles of ape locomotion represent sensitive adaptations to ecological pressures, and remind us that modern human bipedality did not evolve along a steady linear path.

In *Au. sediba*, a southern African species that lived more recently than 2 Ma, internal finger bone structure demonstrates *in vivo* power grasping – evidence of more than just a primitive relic of arboreality. This proven climbing ability existed alongside knee, ankle, and lower back morphology suggestive of bipedalism (Dunmore et al., 2020; Williams et al., 2021). Recent dating of South African fossil sites indicates that this species existed contemporaneously and within a 250 km² area inhabited by both *Paranthropus robustus* and *Homo* aff. *erectus* (Herries et al., 2020). Not only does this highlight the diversity of the Pleistocene hominin family tree, but it once again brings up questions about the role of homology and homoplasy in shaping “unique” features of human morphology. Whilst *Au. sediba* has often been considered to sit between *Au. africanus* and *Homo* in the ancestral tree, the discovery of their contemporaneity suggests it may not be ancestral to *Homo*, in which case their shared features could be homoplastic rather than homologous (Du and Alemseged, 2019; Herries et al., 2020).

Evidence of arboreality persists even beyond the genus *Australopithecus*. There are now analyses of the upper limb of *Paranthropus boisei* suggesting that this species was regularly climbing trees in eastern Africa ~1.5 Ma (Richmond et al., 2020), despite its C₄ diet indicating regular exploitation of terrestrial resources. And a study of the trabecular structure of southern African hominin femurs indicates regular climbing behaviours in a specimen attributed to either *Paranthropus robustus* or *Homo* (Georgiou et al., 2020). Within the genus *Homo*, it appears that 1.8-million-year-old *H. habilis* had forelimbs that were conducive to climbing (Ruff, 2009), a feature that also seems to have been present in *H. naledi*, a southern African hominin that lived as recently as 200 to 400 thousand years ago (Dirks et al., 2017; Feuerriegel et al., 2017). Even from within the past hundred thousand years, we have postcranial evidence from *H. floresiensis* that suggests the small-bodied hominin had a very different gait to its contemporaneous *Homo* species (Harcourt-Smith and Aiello, 2004; Jungers et al., 2009; Larson et al., 2009). Whilst an interpretation of the locomotor style of *H. floresiensis* remains elusive, one analysis of hominin limb joint proportions place *H. floresiensis* in a group with *Au. africanus*,

Au. sediba, *P. robustus*, *P. boisei*, and *H. habilis*, all of which the study describes as having more “ape-like” proportions than those of *Au. afarensis*, *H. erectus*, and *H. naledi* which more closely resemble those of modern humans (Prabhat et al., 2021).

Once again, the analyses above can be criticised for their dichotomous comparison of “ape-like” and “human-like” traits and an over-reliance on extant ape locomotion as a model for extinct species. Furthermore, different methods and interpretations of evidence, as well as the use of different reference skeletons, lead researchers to different and even contradictory conclusions (Chaney et al., 2022; Haeusler and McHenry, 2004; Kramer, 2012; Prang, 2019). However, there is still much to learn from this accumulation of fossil evidence. Not only does it highlight that arboreality was likely present in a diverse range of hominin taxa and across multiple geographic regions and time periods, but it also demonstrates that terrestrial bipedality emerged in different forms, at different times, and in varied combinations with other traits such as larger brains – all contributing to the mosaic nature of hominin evolution (Foley, 2016). *Au. afarensis*, for example, demonstrates a combination of some form of terrestrial bipedalism with a small endocranial volume and ape-like brain organisation (Gunz et al., 2020), and *P. boisei* was clearly exploiting open grasslands but also retains a smaller brain and arboreal adaptations (Falk et al., 2000; Richmond et al., 2020; Sponheimer et al., 2013). Meanwhile *H. habilis* demonstrates a combination of the “typical” larger brain of *Homo* with signals of continued arboreality (Ruff, 2009; Spoor et al., 2015), and *H. naledi* is a relatively recent species of *Homo* but demonstrates a combination of small brain and climbing adaptations (Feuerriegel et al., 2017). Evidence of this locomotor diversity calls attention to the many selective pressures that act and interact to shape behaviour and morphology. It raises questions such as: What were the biotic and abiotic variables that released some primate species from the ancestral state of arboreality? Which of these variables (and the interactions between them) were the strongest drivers of opportunistic terrestriality? And what were the subsequent benefits of opportunistic terrestriality that selected for longer term behavioural and morphological adaptations? Additionally, what dictated the style of locomotion (e.g., bipedalism vs. quadrupedalism, or knuckle-walking vs. palmigrade locomotion) in which a transition to the ground was made by various taxa? These are all questions that can be answered by integrating insights from paleoecology and modern ecosystems to better understand the interactions between primate morphology, behaviour, substrate-use, and ecology.

3 Integrating paleoecological evidence with insights from behavioural ecology

Another reason not to assume signals of arboreality are “relics” is the paleoecological evidence that most hominin species lived in and utilised environments with significant woody cover. Grasslands emerged in eastern Africa ~10 Ma (although see Peppe et al. (2023)

for evidence on Early Miocene habitat heterogeneity), with an increase in the rate of expansion ~4 Ma that can be seen in a significant shift in herbivores' diets by 2 Ma (Cerling et al., 2015; Uno et al., 2016). Whilst hominins emerged alongside these expanding grasslands, their habitats had more tree coverage than previously thought (Negash et al., 2019) and evidence about their diets suggests that they were still utilising more wooded environments even as grasslands expanded (Cerling et al., 2013; Manthi et al., 2020; Senut et al., 2018; Uno et al., 2016). This not only dispels the savannah hypothesis but is a strong indication that the prevalence of trees would have continued to positively select for arboreality, given that it is the ancestral state in primates. Current evidence suggests that it is only after ~2 Ma that the thinning of trees might have become influential in driving more frequent terrestrial locomotion in hominin taxa *Paranthropus* and *Homo* (Levin, 2015; Quinn et al., 2013; Wynn et al., 2020), as well as various papionin taxa (Elton and Dunn, 2020; Jablonski, 1993). This understanding will become more nuanced, and new hypotheses will emerge as we discover paleoecological evidence across greater temporal and geographic scales. For example, recent evidence that the C₃-C₄ transition in eastern Africa might have been "more protracted and complex than elsewhere" (Peppe et al., 2023) highlights the importance of considering localised impacts of vegetation change on animal behaviour, and has already generated new hypotheses about primate locomotion in the Early Miocene (MacLatchy et al., 2023).

Interpreting paleoecological evidence and generating nuanced hypotheses about the relationships between organisms and their environments will benefit greatly from integrating behavioural ecology insights from extant species. For example, the relationship between tree availability, habitat structure, and arboreality can be explored through the study of extant primates. We know that the vast majority of extant primate species are arboreal (approx. 80 – 90%) (Estrada and Marshall, 2024; Galán-Acedo et al., 2019) and are very sensitive to fragmentation of their habitats (Marsh, 2013; Pozo-Montuy et al., 2011), so it is worth studying the factors that influence behaviour in the minority of species termed "terrestrial" or "semi-terrestrial".

Here, Papionini are useful, not only as the primate tribe with the most terrestrial species, but also because certain genera like *Theropithecus* and *Papio* evolved in parallel with hominins, inhabiting similar environments, going through similar diversification patterns, and successfully dispersing across Africa as relatively large-bodied terrestrial primates (Foley, 1993; Gilbert et al., 2018; Hughes et al., 2008; Jolly, 2001; Strum and Mitchell, 1987; Swedell et al., 2012). For example, *P. boisei* and *T. oswaldi* – two C₄ specialists, both approximately 50kg – appear to have existed contemporaneously and sympatrically. The only extant graminivorous primate, *T. gelada*, shares conserved traits with *T. oswaldi*, specialised for eating grasses and sedges, which comprise over 50% of modern geladas' diets. However, observation of geladas shows us that they consume a diverse range of plant species, including digging for underground "fallback foods" which sustain them through drier periods. They also consume invertebrates (a source of protein, fats, and micronutrients), and rarely but

opportunistically eat meat and bird eggs (a behaviour that was seen to spread through the group after years of no instances of egg consumption) (Fashing et al., 2014). These insights about *T. gelada* give us an idea of the dietary complexity, social dynamics, behavioural flexibility and innovation that might have existed in *T. oswaldi* or *P. boisei*, but cannot be seen in the fossil record. Similarly, we know that geladas social and terrestrial behaviours are strongly influenced by predation pressure. They live in the most open environments of any primate but also in the biggest groups (>1,000), probably as a mitigation strategy against predation. When they encounter leopards, gelada groups become more cohesive, and will return to or remain at their sleeping sites (cliffs that provide them refuge off the ground) (Lin et al., 2020). The insights above highlight selective pressures both *for* (access to fallback foods, meat, potential social benefits) and *against* (exposure to predation risk) terrestriality.

Studying extant species also facilitates exploration of factors like predation pressure on behaviours across scales (e.g., from individual animal to troop or population level) and timeframes (e.g., from short-term behavioural adjustment to long-term behavioural patterns that could result in morphological adaptation). For example, the authors of this paper have studied how perceived risk affects baboon terrestriality at multiple scales. At an individual and troop level, our research adds to a body of evidence demonstrating that primates spend more time on the ground when perceived risk is low (Campbell et al., 2005; Hammond et al., 2022; Isbell and Young, 1993; Monteza-Moreno et al., 2020; Mourthé et al., 2007; Nowak et al., 2014). Our study of baboons in southeastern Africa also shows that perceived risk is mediated by habitat structure and temporal variables, and that different behavioural strategies – for example, vocalisations or vigilance – might be deployed dependent on habitat or context (Hammond et al., 2022). This tuning of response to microhabitat variability demonstrates baboons' behavioural flexibility and suggests that groups exposed to even slightly different environments might adopt divergent behavioural repertoires over time, with longer-term consequences including morphological change and even speciation.

At broader scales, remote sensing technologies like camera trapping and GPS-collaring of animals provide insights into population level behaviours. These include inter-troop and inter-specific dynamics. For example, one study used GPS-collaring to find that baboon troops overlapped more with each other when dry periods made them reliant upon evenly-distributed, low-quality fallback foods like grass corms (Markham et al., 2013). This highlights how seasonal fluctuations might have impact on diet, terrestriality (to access the fall-back foods) and social behaviours (due to more inter-troop interactions and perhaps conflict). In a camera trap study across neighbouring populations of baboons, we found fluctuations in baboon terrestriality over both seasonal and circadian cycles, with the latter seemingly influenced by perceived risk in the landscape (Hammond et al., 2025). Seasonally, we found that baboons spent more time on the ground during dry months, perhaps needing to travel further for scarce water resources or fallback foods. And across circadian cycles, baboons were less

terrestrial at dawn and dusk (“riskier” times of day for predator activity), particularly in the environment inhabited by leopards – their primary predator.

These insights from baboon behavioural ecology highlight the importance of studying hominin and papionin fossils in the context of the environments in which they lived. For example, the availability and distance between water sources in their environments could have been a selective pressure for increased terrestriality and/or a limiting factor on the extent of their dispersals (Foley, 2018). The more data we can collect on seasonal patterns and water availability in hominin landscapes, and the more we can integrate studies of the papionins that also inhabited those landscapes (of which there are many more fossil specimens than hominins), the better we will understand how and why some primate taxa might have come to spend more time on the ground than others. The examples above highlight particular value in understanding the natural history of species where we can track both their evolutionary history and modern ecology (e.g., *Theropithecus*), and in cases where we can learn about interactions between behaviour, morphology and ecology at multiple scales and across different contexts (e.g., *Papio*). This can help us move away from focusing on the “uniqueness” of modern human bipedality towards a clearer understanding of the roots and consequences of terrestriality and locomotion in our own lineage but also across the primate order.

3.1 Exploring hominin terrestriality

As discussed, a degree of bipedality has often been attributed to hominin fossils, with species of *Australopithecus* described variously as “committed”, “obligate”, or “habitual” bipeds, and with *Homo* fossils as different as *H. habilis* and *H. erectus* classified as “obligate” bipeds, albeit with the latter distinguished as a “fully committed” biped (Harcourt-Smith, 2016; Ruff, 2009). The difference between these terms has traditionally not been clearly defined and is often inferred from fossil features, rather than a definition of each behaviour *in vivo* (Stamos and Alemseged, 2023). This issue is compounded when interpretations of hominin morphology draw from comparisons with extant species classified as “arboreal”, “semi-terrestrial”, or “terrestrial” – another set of terms without clear definitions (Williams et al., 2023). These terms also overlook the fact that even the most terrestrial of non-human primates engage in relatively frequent arboreal activity, at the very least ascending into trees or cliffs to sleep at night. And conversely, even the most arboreal of non-human primates engage in opportunistic terrestriality (a recent finding only facilitated by remote monitoring because human presence had previously prevented them from coming to the ground) (Estrada and Marshall, 2024). To effectively interpret the primate fossil record, it is thus essential to understand how form relates to function, for example how extant primate morphology relates to proportional substrate-use, and how that function is driven by ecological factors.

In the case of hominins, we must first disentangle bipedality and terrestriality to understand their independent ecological drivers.

Overreliance on reference to extant African apes has created assumptions that their LCA was at least semi-terrestrial, and questions have therefore asked how and when hominins “stood up” from terrestrial knuckle-walking to bipedal striding (Richmond and Strait, 2000; Sayers et al., 2012). However, there is evidence that knuckle-walking in non-human apes might be an example of convergent evolution (Dainton and Macho, 1999; Kivell and Schmitt, 2009), and that hominin bipedality might have an arboreal origin. Proponents of this argument highlight that arboreality provides a relatively secure food supply and security from predators, and fits better with the palaeoecological evidence that hominins emerged in wooded environments (Crompton et al., 2010b; Senut et al., 2018; Thorpe et al., 2007). Furthermore, by broadening the scope of comparative analyses beyond African apes to also incorporate extant orangutan behaviour in interpretations of the fossil record, an argument can be made that arboreal bipedalism might have given the LCA of extant apes an advantageous way of moving about on flexible end-branches of trees. This might explain apes’ shared adaptations to orthograde, as well as the fossil evidence that many early and possible hominins display hindlimb adaptations to bipedalism whilst retaining forelimb adaptations for arboreality (Thorpe et al., 2007). An arboreal origin of ape bipedalism might have been driven by growing competition from monkey species during the middle Miocene. Monkeys can digest less-ripe fruits in the centre of trees, potentially forcing apes to compete by using more suspensory and clambering behaviours to reach riper fruits at the end of branches (Hunt, 2016). Once again, this highlights dynamic aspects of paleoenvironments – competition and niche partitioning – that might have shaped hominin locomotion but cannot be inferred directly from fossils alone.

So, if the evidence increasingly points towards arboreal origins for the hominid LCA, as well as arboreal origins of hominin bipedality, then what and when were the changes that eventually led to a predominantly ground-dwelling *Homo* species? The combined evidence indicates that terrestriality is more common across all extant African great apes than it was in their LCA. Until we have more extensive fossil records for *Gorilla* and *Pan*, we can only hypothesise about the locomotion and postcranial morphology of their ancestors, but they were likely more arboreal than their descendants. For example, we know from extant apes that there is a trade-off between body size and time spent on arboreal travel. Gorillas are both the largest of the non-human apes and the most terrestrial. Male chimpanzees and orangutans are more likely to travel terrestrially than smaller females, and there is some evidence that chimpanzees are more terrestrial than smaller-bodied bonobos (Doran, 1993). Although it is certainly still a matter of debate (Almécija et al., 2021; Grabowski and Jungers, 2017; Williams et al., 2023), if extant African apes are larger bodied than their LCA (and living in more fragmented environments), body size might have been a driver of more terrestrial activity across the clade, but with different locomotor styles that have evolved to fit the different three-dimensional features of their respective environments.

Body mass is very closely linked to terrestriality in primates and has been proposed as a driver of substrate-use. Indeed, in an

analysis of 515 extant primate taxa, body mass was the most reliable predictor of ground use (Estrada and Marshall, 2024). However, when studying extant taxa, it is hard to pinpoint the evolutionary “first movers” in pairs or groups of traits that likely co-evolved. Whilst it might be true that extant primates with bigger bodies spend more time on the ground in modern environments, it is difficult to explain why they would have evolved significantly bigger body sizes in the first place if arboreality and substrate structure constrain body mass. The correlation we see today might thus be a result of increased terrestriality in certain taxa having facilitated the evolution of bigger bodies in those lineages.

3.2 Disentangling the causes, consequences, and correlates of primate terrestriality

Ancestral state reconstructions (ASR) used to estimate how often terrestriality evolved in primates suggest it emerged on at least two separate occasions during the Miocene (within the Cercopithecae lineage ~22–15 Ma and the Hominae lineage ~15–9 Ma) (Estrada and Marshall, 2024). The earliest fossil evidence of terrestriality in Old World primates comes from the Kenyan fossil record at Maboko Island 15 Ma, in both a cercopithecoid, *Victoriapithecus*, and a hominoid, *Equatorius* (formerly known as *Kenyapithecus*). There is no evidence that this emergence of terrestriality was preceded by an opening up of habitats in the region, nor by an increase in the body sizes of either genus. But the fact that adaptations to terrestriality emerged in two separate clades in the early to middle Miocene of Africa does suggest that something about their ecological context was driving substrate-use (McCrossin et al., 1998). This evidence not only highlights that primate terrestriality emerged as early as the Miocene and was independent from bipedality, but it also provides a period and site ripe for further examination of the biotic and abiotic variables that might have driven primates to spend more time on the ground.

Body mass is just one of several factors associated with primate terrestriality. Others include bigger home ranges and social groups, higher male: female ratios within troops, the use of open habitats, warmer and/or drier habitats, lower predation pressure, dietary shifts, and the use of tools (Bandini et al., 2022; Clutton-Brock and Harvey, 1977; Estrada and Marshall, 2024; Fleagle, 2013; Heldstab et al., 2016; Kim et al., 2019; McCrossin et al., 1998; Meulman and van Schaik, 2013; Willems and Van Schaik, 2017; Wright et al., 2019). Many of these characteristics are also central to the study of human “uniqueness”. However, it is difficult to disentangle which, if any, of the factors *cause* an increase in primate terrestriality, and which are *consequences* of more time spent on the ground (McCrossin et al., 1998). Evidence, both from the fossil record and living primates, suggests that many of these traits fall in the latter category.

Data from the “Ecological traits of the world’s primates” database – representative of 504 primate species (Galán-Acedo et al., 2019) – show that more terrestrial species have larger home ranges and inhabit a greater number of habitat types than arboreal species,

with body mass in terrestrial species being an additional predictor of home range size (see [Supplementary Material](#) for analyses). These extant relationships suggest that terrestriality, particularly in combination with an increase in body size, allowed species to disperse further and exploit novel and diverse environments.

Another likely consequence of spending more time on the ground appears to be tool-use (Falótico and Ottoni, 2023; Meulman et al., 2012; Ottoni and Izar, 2008). Once thought to be unique to humans, and specifically to the genus *Homo* (Kivell, 2015; le Gros Clark, 1966), tool-use is now studied in several species across the animal kingdom, and several lines of evidence link it with terrestriality. Tool-use is most prolific amongst primate and bird species that spend a significant amount of time foraging on the ground (Heldstab et al., 2016) and is more common and complex in terrestrial than arboreal settings (Meulman et al., 2012; Visalberghi et al., 2015). Terrestriality is also positively associated with technological diversity, as reflected in variation amongst capuchin populations (Falótico and Ottoni, 2023) and perhaps also in the higher rates and types of tool-use in chimpanzees compared to more arboreal bonobos (Doran, 1993; Samuni et al., 2022). It is thought that terrestriality facilitates more frequent and complex use of technology by increasing individuals’ exposure to a greater range of food and raw materials, as well as providing better opportunities for social learning. The stability of the ground frees up primates’ hands, acts as a more reliable substrate than tree branches for activities like nut cracking, and provides space for juveniles to observe and scrounge from more proficient tool users. Furthermore, the accumulation of materials at specific terrestrial sites increases encounter rates with the materials and settings needed for primates to engage in tool-use, learning, and innovation (Meulman et al., 2012; Ottoni and Izar, 2008; Visalberghi et al., 2015).

Orangutans, the most arboreal of the extant great apes, very rarely make complex tools in the wild, but are able to do so in captivity where they lead more terrestrial lives. This suggests that they are not limited by cognitive factors but by their ecological setting (Meulman and van Schaik, 2013). Baboons are another primate species that use tools in captivity, but not in the wild (Laidre, 2008). This lack of tool-use in the wild is somewhat surprising given their degree of terrestriality, but it serves as a reminder about the complex web of relationships that link ecology with behaviour. Whilst harder to investigate than differences in tool-use across chimpanzee groups, there is some indication that the type of object manipulation exhibited by different baboon groups might vary according to environmental factors (Hamilton et al., 1978). Similarly, whilst highly terrestrial geladas are predominantly granivorous, they also engage in a range of complex foraging behaviours (including digging, cleaning, and peeling various plant foods as well as catching and removing appendages of flying invertebrates), particularly in more intact ecosystems (Fashing et al., 2014). Comparative research could explore this further to understand how terrestriality influences the complexity or frequency of object manipulation and extractive foraging. If terrestriality conferred advantages to certain taxa, it likely drove further adaptation to ground-use as well as co-evolution of cognitive and technological abilities.

One factor that is more clearly a cause of variation in primate substrate-use is the risk of predation – or even just the *perceived* risk of predation. “Landscapes of fear” – the spatial distribution of perceived risk in environments (Gaynor et al., 2019; Palmer et al., 2022) – have been widely studied in modern ecological settings, and are increasingly recognised as having both immediate and long-term effects on the amount of time primates spend on the ground (Campbell et al., 2005; Hammond et al., 2022; Isbell and Young, 1993; Monteza-Moreno et al., 2020; Mourthé et al., 2007; Nowak et al., 2014). Fear of predators is also thought to be the primary driver of one of the most conserved behavioural traits across the primate order: ascending from the ground to sleep at night (Anderson, 1998; Bidner et al., 2018). We must therefore explore the relationships between predators and primate terrestriality throughout evolutionary history. It is also worth considering when and how hominins overcame the fear of predators to the extent that they no longer needed to climb to safety at night. This would surely mark the true transition to a “fully committed” terrestrial biped. The section below discusses methods and issues around studying primate landscapes of fear in the fossil record.

4 Primate terrestriality and landscapes of fear in the fossil record

A major issue with finding trends in fossil and paleoecological data is the extreme spatial and temporal averaging that must be done due to low resolution of the data. We see this in the exploration of paleoenvironments and hominin bipedality; the savannah hypothesis was built and survived on the detection of a general trend towards expanding grasslands that happened over millions of years, in combination with very few and geographically sparse hominin fossils. It has taken finer-scale examination of the environments at each fossil site to highlight that the earliest hominins arose in wooded habitats and maintained climbing adaptations. Similarly, due to the relative rarity of both hominin and carnivore fossils, our understanding of the dynamics between hominins and predators has been built on general and long-term trends. The portrayal of hominin-carnivore dynamics has predominantly focused on the entrance of hominins to the carnivorous niche rather than on hominins’ vulnerability to predation by the various large terrestrial carnivores roaming the landscape, as well as other predators such as crocodiles or raptors (Hopwood, 2014; Werdelin and Lewis, 2013b). There is a detectable trend showing that carnivore abundance and diversity in eastern Africa peaked ~3.5 Ma, and was followed by a clear decline towards the present, with a particularly dramatic drop in both the abundance and diversity of species ~1.8 Ma (Lewis and Werdelin, 2007; Werdelin and Lewis, 2005, 2013b). Broadly coincident with the emergence of *H. erectus* and a shift towards more sophisticated Acheulean technology, researchers have proposed that hominin technology and competition drove this wave of carnivore extinctions (Lewis and Werdelin, 2007; Ripple and Van Valkenburgh, 2010; Werdelin and Lewis, 2013b; Willems and Van Schaik, 2017).

However, the development of hominin carnivory (as inferred from the archaeological record) is still a matter of much debate. There are big questions to be answered about whether hominin meat-eating stems from hunting or scavenging origins (Blumenschine, 1986; Domínguez-Rodrigo and Pickering, 2003; Pickering and Bunn, 2007; Pobiner, 2020; Shipman, 1986; Thompson et al., 2019). There are also arguments that we have overestimated the importance of meat in early hominin diets due to the preservation bias of stone tools compared to perishable technology and other behavioural indicators of diet in the fossil record (Espigares et al., 2019; Pascual-Garrido and Almeida-Warren, 2021). And although there is a shift from Oldowan to more advanced Acheulean technology ~1.76 Ma, the tools are evidence of butchery but not of how hominins were accessing carcasses, especially enough to outcompete other carnivores. Furthermore, recent analyses of cut-marked bones suggest that the inferred increase in meat-eating shortly after 2 Ma might in fact be a sampling artefact (Barr et al., 2022). Together, all this evidence indicates that hominins might not have been outcompeting carnivores and driving them to extinction by 1.8 Ma.

Whilst the timing and importance of meat-eating in hominins will continue to be a topic of much debate and research, the broad trend showing the decline of carnivores should also be explored from the opposite angle. Regardless of cause, what would these significant carnivore extinctions have meant for hominins and other primates? The decline from peak abundance and diversity of carnivores 3.5 Ma, and the more rapid decline after 1.8 Ma coincides roughly with the emergence and survival of increasingly terrestrial hominins. Perhaps declining predation risk eased selection pressures for arboreality, allowing hominins to spend more time on the ground? Of course, this is very hard to detect or even imagine at a continental scale and in the context of millions of years. Especially as we know from extant primates that risk can affect terrestriality in a localised way, both temporally and geographically.

For example, long-term observation of a population of northern muriquis (*Brachyteles hypoxanthus*) documented a 20-fold increase in their terrestrial activity over 23 years. This included a notable increase in nonessential terrestrial activities like resting and socialising, and a growth in group size from ~20 to 80 individuals. This shift in substrate-use did not appear to be driven by availability of trees but by a shift in these monkeys’ landscape of fear over the course of habituation. The presence of researchers likely reduced the monkeys’ perceived risk of humans over time, and deterred their predators, possibly also accompanied by a decline in the predator population over the multi-decadal research (Tabacow et al., 2009).

Remote-sensing studies also provide insights about localised impacts of landscapes of fear. For example, our camera trap study introduced in Section 3 revealed that baboons spent more time on the ground during crepuscular and nocturnal hours in an environment with low predation risk (P. Hammond et al., 2025). Risk can also vary depending on the particular predator species and hunting styles present in a landscape. For example, a study that used GPS-collars to simultaneously track leopards (*Panthera pardus*),

vervet monkeys (*Chlorocebus pygerythrus*), and olive baboons (*Papio anubis*) found that the leopards appeared to target the two primate species at different times of day. Leopards preferentially hunted smaller-bodied vervets during the day whilst actively avoiding baboons, who are known to attack and even kill leopards. However, the leopards then targeted the larger-bodied baboons (which fall within leopards' preferred prey size) at night, when detection and pre-emptive attack by the baboons were less likely (Isbell et al., 2018). This highlights how risk of predation can change across the diel period, and why primates might be particularly affected by the presence of a particular predator species within the landscape. Indeed, collar data from the same field site showed that baboons very rarely departed their sleep sites before sunrise and that they left sites significantly later on mornings after a leopard had been in proximity (Bidner et al., 2018).

Findings from behavioural ecology research thus provide nuanced insights into how activity might be shaped by decreased predation pressure in a landscape. For example, if there is a loss of large carnivores – even just one or two key species – from an ecosystem, it might relax the landscape of fear and increase primate terrestriality, particularly around crepuscular and nocturnal hours. Primates might then be able to utilise these hours for extra travel, foraging, or socialising, all during the coolest parts of the day. If these activities confer advantages to groups of primates who can more flexibly utilise the ground, there could be further selection for terrestrial behaviour and even ultimately morphological adaptations to terrestriality.

These insights also generate further questions. From the behavioural ecology angle, it is necessary to unpick the consequences of terrestriality in primates, particularly around opportunities for more extensive exploration of the environment, object-manipulation, group cohesion, and social behaviours. And from the human evolution angle, understanding the emergence of terrestrial bipedalism will require more careful and localised investigation of the predator guilds at different sites that contain hominid, hominin, or papionin fossils from the Miocene and Plio-Pleistocene. Although methodologically difficult, it will also be beneficial to identify the particular carnivore species that might have been the primary predators of different primate species over time. Rather than trying to examine the effects of continent-wide carnivore extinction rates on human evolution, identifying these key predators and using site-specific research to pinpoint their localised presence/absence will provide an avenue for exploring shifting landscapes of fear and the downstream consequences of reduced risk on primate behaviour.

4.1 Evidence of carnivore damage to primate fossils

One avenue for further exploration is to examine primate fossils for tooth or claw marks. The Taung assemblage in South Africa, which includes the skull of an *Australopithecus africanus* infant, is likely to have been accumulated by a large bird of prey ~2.5 Ma (Berger and Clarke, 1995; McGraw et al., 2006), which serves as a

reminder that hominins faced threats beyond large terrestrial carnivores, including raptors and crocodiles (Njau and Blumenschine, 2012). Many other assemblages that contain primate fossils – particularly in South Africa – show strong signals of carnivore activity, although it is difficult to determine which carnivores were responsible for marks observed on bones (DeSilva et al., 2013; Fourvel et al., 2018; Pickering et al., 2004; Val et al., 2014). For example, the Cooper's D assemblage in South Africa contains a large proportion of large-bodied primate fossils, accumulated in a cave ~1.5 Ma. Fossilised primate genera include *Papio*, *Theropithecus*, *Gorgopithecus*, and *Paranthropus*, with 6.2% of the primate bones showing carnivore damage, including a mandibular fragment from *P. robustus* (Val et al., 2014). This has been attributed to leopards or hyenas based on comparisons with modern examples of bone damage, but the site was also inhabited by sabertooth cats, *Megantereon* and *Dinofelis*, whose signatures might be harder to detect due to a lack of a modern comparison (Val et al., 2014). At Swartkrans, a tooth-marked *P. robustus* cranium has also been attributed to leopard predation (Brain, 1981). However, isotopic analyses from carnivores at the site indicate that *Megantereon* and *Crocota* species, as well as leopards, are all possible candidates for predators of the hominins and baboons at that site (Lee-Thorp et al., 2000).

Predators appear to have been less actively involved in the accumulation of Plio-Pleistocene fossils at eastern African hominin sites than southern African ones. However, there is still some evidence of likely carnivore damage to several hominin fossils from eastern Africa. These include signs of possible leopard predation on *Orrorin tugenensis* 6 Ma (Gommery et al., 2007), carnivore damage to *Ardipithecus ramidus* bones 4.4 Ma (Woldegabriel et al., 1994), and both crocodilian and mammalian carnivore damage to *Homo habilis* fossils 1.8 Ma (Njau and Blumenschine, 2012). Signs of fossil damage indicate that hominins continued to face threats of predation as they dispersed out of Africa (Margvelashvili et al., 2022) and through the recent past to the modern day (Camarós et al., 2016; Hart and Sussman, 2011). Whilst more research is needed to improve identification of specific predators from marks that they leave on bones, the presence of the marks themselves highlights the importance of considering the landscape of fear as an influential driver of behavioural evolution in hominins and other primate lineages.

4.2 Plio-Pleistocene carnivore behaviour

Beyond identifying key predators of different primate species, advancing methods provide insights into other aspects of landscapes of fear throughout evolutionary history. Carnivorous fossil morphology reveals a lot about hunting styles and niche partitioning amongst guild members through time. For example, sabertooth predators have evolved multiple times throughout evolutionary history, in different families (another example of homoplasy). Compared to the more versatile diets of extant carnivores, sabertooths are characterised as hypercarnivores with dentition so specialised for cutting meat that they could not

consume bone or other food items. Although often characterised as targeting megaherbivores, there is stronger evidence to suggest that they targeted medium-sized herbivores but had adaptations to perform quicker kills and more efficient stripping of meat from carcasses than conical-toothed cats (Mauricio, 2013). Amongst sabertooth taxa, there appear to have evolved two general “ecomorphs”, or strategies, for hypercarnivory. “Dirktooth” predators had very long sabers and a muscular build suited to a more solitary, ambush hunting strategy, likely conducted in closed environments. “Scimitar-tooths” on the other hand were more gracile with longer limbs and greater speed to pursue prey, likely hunting in more open environments and perhaps in groups (Mauricio, 2013). Building on this, isotopic analyses provide evidence that scimitar cats, such as the early Pleistocene *Homotherium*, were coursing predators that hunted predominantly large-bodied herbivores in open habitats. Meanwhile, dirktooth cats such as *Megantereon* were ambush hunters of browsers in closed habitats (Palmqvist et al., 2008). The inferred features of *Megantereon* indicate that it might once have filled a similar niche to the modern-day leopard, perhaps making it a key predator of medium to large-bodied primates – including early hominins.

Whilst informative, the examples above serve as a reminder that there are many features of these ancient landscapes of fear that do not have modern analogues, making it difficult to do more than hypothesise about the prey preferences and hunting techniques of animals like sabertooth cats, very large hyenas, and short-faced bears (Hart and Sussman, 2011; Van Valkenburgh et al., 2016). Additionally, whilst Africa has the most intact and diverse predator guild of the modern day (Cozzi et al., 2012; Dalerum et al., 2009), evidence from the eastern African fossil record suggests that the functional richness within the guild has declined by almost 99% since 3.5 Ma (Werdelin and Lewis, 2013b). This makes it difficult to imagine how prey species might have been affected by a far greater diversity of carnivores and very different intraguild dynamics. For example, Pleistocene ecosystems were home to many large (>100kg) hypercarnivores, several of which lived sympatrically. Today, only lions and tigers fill this niche and they do not overlap geographically. These differences in the make-up of extant and extinct carnivore guilds suggest that prey species, including primates, probably inhabited much more salient and complex landscapes of fear than exist today. On the other hand, predation pressure might actually be heightened in some modern ecosystems compared to paleo environments. This is because anthropogenically-induced habitat fragmentation and restricted-size reserves (protected areas that are smaller than naturally functioning ecosystems) might create more concentrated or “artificial” spatial overlap amongst carnivores and prey species compared to what would exist in an environment unmarred by modern human activity (Hayward and Slotow, 2009; Searle et al., 2021). This highlights the need to study community-level dynamics like predation and competition and how they interact with the diversity and intactness of an ecosystem. A better understanding of ecosystem regulation and trophic cascades is not only crucial for conservation of modern environments, but also to learn about

significant ecological shifts in evolutionary history (Estes et al., 2011; Terborgh et al., 2001).

If fed into a more integrated and cyclical feedback loop, advances in both paleontology and behavioural ecology will contribute to increasingly accurate models of past landscapes of fear. From these we can then generate insights and hypotheses about the role of risk in behavioural evolution. The collection of more fossil evidence will provide us with information on which prey species were vulnerable to certain predators, and will increase the resolution of data about presence and abundance of carnivore species through time and space. Meanwhile, advances in remote sensing and community-level ecology will expand our understanding of extant intraguild dynamics and their effects on entire ecosystems, which could perhaps then be modelled in hypothetical environments without the artificial constraints of national borders or park boundaries.

4.3 Fossil sites for future research

Whilst it will take time to build increasingly accurate models of these broad paleo environments, there are particular sites at which localised patterns of carnivore speciation, extinction, and primate substrate-use might be studied. As discussed, primate terrestriality emerges in two primate clades at Maboko Island, Kenya, ~15 Ma. The simultaneous emergence of the characteristic in both the *Victoriapithecus* and *Equatorius* lineages precedes the expansion of grasslands in the region and appears to have happened when both taxa were relatively small-bodied (McCrossin et al., 1998). In the case of *Equatorius*, morphological analyses indicate that it likely engaged in palmigrade terrestrial locomotion which evolved independently to adaptations like the knuckle-walking seen in living hominoids (Patel et al., 2009). Researchers have hypothesised that a shift in diet might have caused the terrestriality seen in the lineages at Maboko Island (McCrossin et al., 1998). This hypothesis should be explored alongside considerations of pressures – including predation – that would have deterred them from descending to the ground. Perhaps the emergence of primate terrestriality was preceded by a drop in either the abundance or diversity of predators at the site? If temporal resolution is too low to explore sequential patterns at the site, the inferred landscape of fear at Maboko Island could be compared to those of other sites from a similar time period to investigate whether there were unusually low numbers of carnivores in the Maboko region ~15 Ma. It would also be a good site to study primate fossils more closely for carnivore damage, both as a proxy for predation rate amongst the sample and to identify key predators of primates at the site.

A similar example exists at Koobi Fora and surrounding deposits in the Omo-Turkana Basin, where the fossil record captures increasing terrestriality in both hominins and the cercopithecoid genus, *Theropithecus*, over millions of years (Bobe et al., 2022; Cerling et al., 2013; Jablonski, 1993). Koobi Fora has yielded vast records of paleoclimatic, fossil, and archaeological materials representative of millions of years of ecological and technological transitions in the area (Bobe et al., 2022; Feibel, 2011). It is an excellent site for integrating evidence over broad

geographic and temporal scales, with sediment layers ranging from 4.3 to 0.6 Ma, and with discrete subsections that can be geochemically matched across formations, allowing researchers to analyse temporal correlations of materials found across the Omo-Turkana region (Gathogo and Brown, 2006; Jablonski et al., 2008; Rogers et al., 1994).

The Koobi Fora record captures several longitudinal trends. It documents the presence of *Au. anamensis* ~4 Ma and the high diversity when *H. habilis*, *H. rudolfensis*, *H. erectus*, and *P. boisei* occupied the region between 2 and 1.4 Ma (Bobe et al., 2022). Its archaeological record demonstrates a shift from a few Oldowan sites before 1.9 Ma (Braun et al., 2010), through the transition to Acheulean technology 1.76 Ma (Lepre et al., 2011), to an abundance of many sites with large numbers of artefacts spread across the landscape by 1.5 Ma (Presnyakova et al., 2018; Rogers et al., 1994). This increase in production of lithic technology is proof that hominins were spending a significant amount of time on the ground by 1.5 Ma. It is worth exploring whether or when their levels of terrestriality decoupled from trends seen in other primate lineages at the site. For example, Koobi Fora also documents a rise in the numbers of *Theropithecus*, a primate genus that became increasingly terrestrial and widespread until it was the most common primate in the landscape by 1.5 Ma (Bobe et al., 2022; Jablonski, 1993). Broadly, the increasing terrestriality in both *Theropithecus* and hominins indicates that they were facing similar selection pressures. Indeed, Koobi Fora provides evidence of a shift from wooded environments to more open grasslands, particularly after 2 Ma (Bobe et al., 2022). It also provides evidence of the decline in both the functional and taxonomic diversity of the large carnivore guild in the area, between 2 and 1.5 Ma (Werdelin and Lewis, 2013b, 2013a) which might have released restrictions on primate terrestriality. Future work will need to examine the relationships between carnivore and primate fossils from the site at higher temporal and spatial resolution, aided by new fossil discoveries, improved methodologies, and integrated insights.

As evidenced by studies of extant primate terrestriality, a behavioural shift can arise in a relatively short period of time within a small population of animals and a localised ecological setting. Over the course of primate evolutionary history, there have likely been various spatiotemporal pockets in which the “right” ecological factors have come together to favour terrestrial behaviour in primates, sometimes lasting long enough to shift species’ behaviour or even morphology. Using this behavioural ecology lens, we can better explore how locomotor diversity arose in Miocene and Plio-Pleistocene primates, and we might be able to pinpoint the conditions or place where terrestrial bipedalism emerged in our own lineage.

5 Discussion

There has been a big focus on hominin bipedality as a defining feature of our lineage. In this paper, we summarise the trends that informed early theories about the emergence of “obligate bipedalism” in hominins. We extend our review to include broader timescales (examining the primates and

paleoenvironments of the Miocene), a wider range of taxa (exploring the roots and drivers of terrestriality across a broader set of the primate order), and an integrated set of methods and disciplines for generating and testing evolutionary hypotheses (combining applied insights from behavioural ecology with paleontology and paleoecology).

Whilst many herbivorous taxa adapted to climate change in the Miocene with significant changes to their dentition, Miocene apes appear to have retained their diet and dentition and instead diversified their ways of moving around to forage in the changing environment (Senut et al., 2018). Amidst this diversity lies the origins of hominid locomotion, potentially in a clambering quadruped, likely smaller and more arboreal than its descendants. Hominin locomotion also appears to have gone through a period of morphological diversity, with most hominin taxa retaining more arboreal adaptations than previously assumed, even as terrestrial bipedality emerged.

This complexity at the roots of hominin locomotion is a reminder that we should not search for “morphological intermediates” between modern great apes and humans to define their LCAs, nor should we overlook the role of homoplasy in shaping evolution. There is increasing evidence that the semi-terrestrial locomotor styles of extant hominids evolved independently, that hominin bipedalism might have arboreal origins, and that both terrestriality and bipedality might have arisen multiple times – independently of one another – in different lineages and places. To understand this diverse and mosaic story, we cannot rely on static fossil evidence, but must incorporate behavioural ecology to consider the dynamic selection pressures faced by hominins and other primates.

In this paper, we argue that the landscape of fear is a key selection pressure that has shaped primate locomotion. We propose that the dramatic loss in carnivore abundance and diversity over the past three million years has allowed all African apes – as well as several papionins – to become more terrestrial than their LCAs, albeit with different styles of locomotion. Our paper reviews the correlates, causes, and consequences of terrestriality, highlighting how localised shifts in predation pressure might have had downstream consequences on primate body mass, group size, social dynamics, ranging and dispersal behaviours, and tool-use.

Future avenues for behavioural ecology research should include exploration of:

- Drivers of terrestriality in non-human primates, with a particular focus on the effects of risk. Papionins, as the most terrestrial tribe, provide both longitudinal fossil evidence across several taxa, as well as examples of extant species that display behavioural flexibility and have successfully dispersed across a variety of habitats.
- Consequences of terrestriality in non-human primates, including on body shape and size, group dynamics, social behaviours, object manipulation, tool-use and meat eating. It is important to study these factors outside of the hominin lineage to avoid biases created by an overrepresentation of stone tools as indicators of hominin behaviour.

- Multi-scale manifestations of behaviour to understand how behaviour is evoked in individuals and how that translates to a troop or population level, and how that translation influences inter-group dynamics and inter-specific differences. In this way, we can build hypotheses about the mechanisms that translate short term behaviours (e.g. opportunistic terrestriality) into evolutionary adaptations (e.g. morphological change in foot shape).
- Hunting strategies, prey preferences, success rates, and broader behaviours of predators in different ecological contexts. If we can understand how predator behaviours are influenced by their environment, and also by intraguild dynamics, we can better model landscapes of fear for both extant and extinct primate species.
- Population and community dynamics including the effects of both competition and predation amongst species, the up and downstream consequences of predator diversity and/or prey diversity in an environment, and the trophic cascades that influence the faunal and floral composition of an ecosystem.

Simultaneously, ongoing fossil discoveries and new perspectives on paleontological and paleoecological data will help us learn more about:

- Diversity at the roots of both hominid locomotion in the Miocene and hominin locomotion in the Plio-Pleistocene. Whilst this paper reviews the diversity of ape locomotion seen across these time periods, new discoveries and advancing methods will bring much greater nuance to our interpretations of ape evolution. Fossil evidence from a broader range of hominid taxa will also reduce our reliance on the “Chimpanzee Referential Doctrine” for hypothesising about different evolutionary branches of the hominid and hominin clades.
- Localised ecological and faunal context at sites where primate terrestriality emerged or persisted. As proposed in this paper, Maboko Island and Koobi Fora are two ideal African fossil sites for in-depth investigation of the habitats, resources, competitors and predators that existed in the landscapes of various papionins and hominins.
- Hunting styles, prey preferences, presence and diversity of predators throughout the Miocene and Plio-Pleistocene and in various ecological contexts. These insights will come from studying both the morphology of carnivoran fossils, and evidence from potential prey fossils such as tooth or claw marks, and bone accumulation patterns.
- Localised carnivore presence and extinction events across Africa. If we can improve the geographic and temporal resolution with which we document these events, we will be better equipped to model shifts in localised landscapes of fear, as well as the consequent behavioural changes in prey species.

Additionally, we need greater integration of the methods and insights from the research avenues above, both through collaborative interdisciplinarity and combined with advanced

modelling approaches. This will facilitate iterative generation of hypotheses and testing across disciplines to better inform our understanding of primate evolution and diversification, and perhaps provide clues about how terrestriality has contributed to human “uniqueness”.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author/s.

Author contributions

PH: Conceptualization, Formal analysis, Project administration, Writing - original draft, Writing - review & editing. RB: Conceptualization, Data curation, Supervision, Writing - original draft, Writing - review & editing, Methodology. SC: Conceptualization, Data curation, Supervision, Writing - original draft, Writing - review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2025.1473794/full#supplementary-material>

References

- Alba, D. (2010). Cognitive inferences in fossil apes (Primates, Hominoidea): does encephalization reflect intelligence. *J. Anthropol. Sci.* 88 Available online at: https://www.isita-org.com/jass/contents/2010vol88/pdfonline/jass2010_05_alba.pdf.
- Alexander, R. (1990). How did humans evolve? Reflections on the uniquely unique species. Available online at: https://deepblue.lib.umich.edu/bitstream/handle/2027.42/57178/SpecPub_001.pdf (Accessed April 9, 2025).
- Almécija, S., Hammond, A. S., Thompson, N. E., Pugh, K. D., Moyà-Solà, S., and Alba, D. M. (2021). Fossil apes and human evolution. *Science* 372. doi: 10.1126/SCIENCE.ABB4363/ASSET/095FDD9D-3280-4DBF-A2B2-FC05ACE166A7/ASSETS/GRAPHIC/372_ABB4363_FA.JPEG
- Almécija, S., Tallman, M., Alba, D., Pina, M., Moyà-Solà, S., and Jungers, W. (2013). The femur of *Ororin tugenensis* exhibits morphometric affinities with both Miocene apes and later hominins. *Nat. Commun.* 4, 1–12. doi: 10.1038/ncomms3888
- Anaya, A., Patel, B. A., Orr, C. M., Ward, C. V., and Almécija, S. (2021). Evolutionary trends of the lateral foot in catarrhine primates: Contextualizing the fourth metatarsal of *Australopithecus afarensis*. *J. Hum. Evol.* 161, 103078. doi: 10.1016/j.jhevol.2021.103078
- Anderson, J. R. (1998). Sleep, sleeping sites, and sleep-related activities: Awakening to their significance. *Am. J. Primatology* 46, 63–75. doi: 10.1002/(SICI)1098-2345(1998)46:1<63::AID-AJP5>3.0.CO;2-T
- Andrews, P. (2020). Last common ancestor of apes and humans: morphology and environment. *Folia Primatologica* 91, 122–148. doi: 10.1159/000501557
- Bandini, E., Harrison, R., and Motes-Rodrigo, A. (2022). Examining the suitability of extant primates as models of hominin stone tool culture. *Humanities Soc. Sci. Commun.* 9, 1–18. doi: 10.1057/s41599-022-01091-x
- Barr, W. A., Pobiner, B., Rowan, J., Du, A., and Faith, J. T. (2022). No sustained increase in zooarchaeological evidence for carnivory after the appearance of *Homo erectus*. *Proc. Natl. Acad. Sci.* 119, e2115540119. doi: 10.1073/PNAS.2115540119/-/DCSUPPLEMENTAL
- Begun, D. R. (2015). “The real planet of the apes: A new story of human origins,” in *The Real Planet of the Apes* (Princeton University Press). doi: 10.1515/9781400874279
- Begun, D. R., Nargolwalla, M. C., and Kordos, L. (2012). European miocene hominids and the origin of the african ape and human clade. *Evolutionary Anthropology* 21, 10–23. doi: 10.1002/EVAN.20329/FORMAT/PDF
- Behrensmeyer, A. K. (2006). Climate change and human evolution. *Science* 311, 476–478. doi: 10.1126/SCIENCE.1116051/ASSET/3F7C7E98-7D87-4100-96ED-B1CD6884A321/ASSETS/GRAPHIC/476-1.GIF
- Berger, L. R., and Clarke, R. J. (1995). Eagle involvement in accumulation of the Taung child fauna. *J. Hum. Evol.* 29, 275–299. doi: 10.1006/JHEV.1995.1060
- Bibi, F. (2011). Mio-pliocene faunal exchanges and african biogeography: the record of fossil bovids. *PLoS One* 6. doi: 10.1371/JOURNAL.PONE.0016688
- Bidner, L., Matsumoto-Oda, A., and Isbell, L. (2018). The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. *Am. J. Primatology* 80, e22932. doi: 10.1002/AJP.22932
- Blumenshine, R. J. (1986). Carcass consumption sequences and the archaeological distinction of scavenging and hunting. *J. Hum. Evol.* 15, 639–659. doi: 10.1016/S0047-2484(86)80002-1
- Bobe, R., and Carvalho, S. (2019). Hominin diversity and high environmental variability in the Okote Member, Koobi Fora Formation, Kenya. *J. Hum. Evol.* 126, 91–105. doi: 10.1016/j.jhevol.2018.10.012
- Bobe, R., Coelho, J., Carvalho, S., and Leakey, M. (2022). “Early Hominins and Paleoeology of the Koobi Fora Formation, Lake Turkana Basin, Kenya,” in *African Paleoeology and Human Evolution* (Cambridge University Press).
- Bobe, R., Manthi, F. K., Ward, C. V., Plavcan, J. M., and Carvalho, S. (2020). The ecology of *Australopithecus anamensis* in the early Pliocene of Kanapoi, Kenya. *J. Hum. Evol.* 140, 102717. doi: 10.1016/j.jhevol.2019.102717
- Böhme, M., Spassov, N., Fuss, J., Tröschler, A., Deane, A. S., Prieto, J., et al. (2019a). A new Miocene ape and locomotion in the ancestor of great apes and humans. *Nature* 575, 489–493. doi: 10.1038/s41586-019-1731-0
- Böhme, M., Spassov, N., Fuss, J., Tröschler, A., Deane, A. S., Prieto, J., et al. (2019b). A new Miocene ape and locomotion in the ancestor of great apes and humans. *Nature* 575, 489–493. doi: 10.1038/s41586-019-1731-0
- Brain, C. K. (1981). *Evolution of man in Africa: Was it a consequence of cainozoic cooling. Annexure to Trans. Geol. Soc. S. Afr.* Vol. 84 (South Africa).
- Braun, D. R., Rogers, M. J., Harris, J. W., and Walker, S. J. (2010). “Quantifying Variation in Landscape-Scale Behaviors: The Oldowan from Koobi Fora,” in *New Perspectives on Old Stones* (Springer New York), 167–182. doi: 10.1007/978-1-4419-6861-6_7
- Brunet, M., Guy, F., Pilbeam, D., Mackaye, H., and Likies, A. (2002). A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418, 145–151. doi: 10.1038/nature00879
- Camarós, E., Cueto, M., Lorenzo, C., Villaverde, V., and Rivals, F. (2016). Large carnivore attacks on hominins during the Pleistocene: a forensic approach with a Neanderthal example. *Archaeological Anthropological Sci.* 8, 635–646. doi: 10.1007/S12520-015-0248-1/FIGURES/4
- Campbell, C. J., Aureli, F., Chapman, C. A., Ramos-Fernández Pronatura Peninsula de Yucatan, G., Matthews, K., and Behavior, T. (2005). Terrestrial behavior of atele spp. *Int. J. Primatology* 26, 1039–1051. doi: 10.1007/s10764-005-6457-1
- Cerling, T., Andanje, S., Blumenthal, S., Brown, F., Chritz, K., Harris, J., et al. (2015). Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. *Proc. Natl. Acad. Sci.* 112, 11467–11472. doi: 10.1073/pnas.1513075112
- Cerling, T., Chritz, K. L., Jablonski, N., Leakey, M. G., and Manthi, F. K. (2013a). Diet of *theropithecus* from 4 to 1 ma in Kenya. *Proc. Natl. Acad. Sci. United States America* 110, 10507–10512. doi: 10.1073/PNAS.1222571110/SUPPL_FILE/PNAS.201222571SI.PDF
- Cerling, T., Manthi, F., Mbua, E., Leakey, L., Leakey, M., Leakey, R., et al. (2013b). Stable isotope-based diet reconstructions of Turkana Basin hominins. *Proc. Natl. Acad. Sci.* 110, 10501–10506. doi: 10.1073/pnas.1222568110
- Cerling, T. E., Wynn, J. G., Andanje, S. A., Bird, M. I., Korir, D. K., Levin, N. E., et al. (2011). Woody cover and hominin environments in the past 6 million years. *Nature* 476, 51–56. doi: 10.1038/nature10306
- Chaney, M. E., Ruiz, C. A., Meindl, R. S., and Lovejoy, C. O. (2022). The foot of the human-chimpanzee last common ancestor was not African ape-like: A response to Prang (2019). *J. Hum. Evol.* 164, 102940. doi: 10.1016/j.jhevol.2020.102940
- Chapman, C. A., and Huffman, M. A. (2018). Why do we want to think humans are different? *Anim. Sentience* 3 (23), 1. doi: 10.51291/2377-7478.1358
- Clutton-Brock, T., and Harvey, P. (1977). Primate ecology and social organization. *J. Zool.* 183, 1–39. doi: 10.1111/j.1469-7998.1977.tb04171.x
- Cote, S. (2004). Origins of the African hominoids: an assessment of the palaeobiogeographical evidence. *Comptes Rendus Palevol* 3, 323–340. doi: 10.1016/j.crpv.2004.03.006
- Cozzi, G., Broekhuis, F., McNutt, J. W., Turnbull, L. A., Macdonald, D. W., and Schmid, B. (2012). Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa’s large carnivores. *Ecology* 93 (12), 2590–2599. doi: 10.1890/12-0017.1
- Crompton, R. H., Sellers, W. I., and Thorpe, S. K. S. (2010a). Arboreality, terrestriality and bipedalism. *Philos. Trans. R. Soc. B: Biol. Sci.* 365, 3301–3314. doi: 10.1098/RSTB.2010.0035
- Crompton, R. H., Sellers, W. I., and Thorpe, S. K. S. (2010b). Arboreality, terrestriality and bipedalism. *Philos. Trans. R. Soc. B: Biol. Sci.* 365, 3301–3314. doi: 10.1098/rstb.2010.0035
- Dainton, M., and Macho, G. (1999). Did knuckle walking evolve twice? *J. Hum. Evol.* 36, 171–194. doi: 10.1006/jhev.1998.0265
- Dalerum, F., Cameron, E. Z., Kunkel, K., and Somers, M. J. (2009). Diversity and depletions in continental carnivore guilds: Implications for prioritizing global carnivore conservation. *Biol. Lett.* 5, 35–38. doi: 10.1098/RSTB.2008.0520
- Dart, R. (1925). *Australopithecus africanus* the man-ape of South Africa. *Nature* 115, 195–199. doi: 10.1038/115195a0
- Dart, R. A. (1925). *Australopithecus africanus*: The man-ape of South Africa. *Nature* 115, 195–199. doi: 10.1038/115195A0
- Dart, R. (1949). The predatory implement technique of *Australopithecus*. *Am. J. Phys. Anthropology* 7, 1–38. doi: 10.1002/AJPA.1330070103
- Darwin, C. (1871). *The descent of man in relation to sex* (London: John Murray).
- Daver, G., Guy, F., Mackaye, H. T., Likies, A., Boissier, J. R., Moussa, A., et al. (2022). Postcranial evidence of late Miocene hominin bipedalism in Chad. *Nature* 609, 94–100. doi: 10.1038/s41586-022-04901-z
- de Bonis, L., and Koufos, G. D. (2014). First discovery of postcranial bones of *Ouranopithecus macedoniensis* (Primates, Hominoidea) from the late Miocene of Macedonia (Greece). *J. Hum. Evol.* 74, 21–36. doi: 10.1016/j.jhevol.2014.05.015
- DeSilva, J. M., McNutt, E., Benoit, J., and Zipfel, B. (2019). One small step: A review of Plio-Pleistocene hominin foot evolution. *Am. J. Phys. Anthropology* 168, 63–140. doi: 10.1002/AJPA.23750
- DeSilva, J. M., Shoreman, E., and MacLatchy, L. (2006). A fossil hominoid proximal femur from Kikorongo Crater, southwestern Uganda. *J. Hum. Evol.* 50, 687–695. doi: 10.1016/j.jhevol.2006.01.008
- DeSilva, J. M., Steininger, C. M., and Patel, B. A. (2013). Cercopithecoid primate postcranial fossils from Cooper’s D, South Africa. *Geobios* 46, 381–394. doi: 10.1016/j.geobios.2013.07.001
- DeVore, I., and Tooby, J. (1987). “The reconstruction of hominid behavioral evolution through strategic modeling,” in *The Evolution of Human Behavior: Primate Models*. Ed. W. Kinzey (Sunny Press). 183–237.

- Dirks, P. H., Kibii, J. M., Kuhn, B. F., Steininger, C., Churchill, S. E., Kramers, J. D., et al. (2010). Geological setting and age of Australopithecus sediba from southern Africa. *Science* 328, 205–208.
- Dirks, P., Roberts, E. M., Hilbert-Wolf, H., Kramers, J. D., Hawks, J., Dosseto, A., et al. (2017). The age of homo naledi and associated sediments in the rising star cave, South Africa. *ELife* 6. doi: 10.7554/ELIFE.24231
- Dominguez-Rodrigo, M., and Pickering, T. (2003). Early hominid hunting and scavenging: A zooarcheological review. *Evolutionary Anthropology* 12, 275–282. doi: 10.1002/EVAN.10119
- Doran, D. M. (1993). Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. *Am. J. Phys. Anthropology* 91, 83–98. doi: 10.1002/AJPA.1330910106/FORMAT/PDF
- Du, A., and Alemseged, Z. (2019). Temporal evidence shows Australopithecus sediba is unlikely to be the ancestor of Homo. *Sci. Adv.* 5. doi: 10.1126/SCIADV.AAV9038/SUPPL_FILE/AAV9038_SM.PDF
- Dunmore, C. J., Skinner, M. M., Bardo, A., Berger, L. R., Hublin, J.-J., Pahr, D. H., et al. (2020). The position of Australopithecus sediba within fossil hominin hand use diversity. *Nat. Ecol. Evol.* 4 (7), 911–918. doi: 10.1038/s41559-020-1207-5
- Elton, S., and Dunn, J. (2020). Baboon biogeography, divergence, and evolution: Morphological and paleoecological perspectives. *J. Hum. Evol.* 145, 102799. doi: 10.1016/j.jhevol.2020.102799
- Espigares, M. P., Palmqvist, P., Guerra-Merchán, A., Ros-Montoya, S., García-Aguilar, J. M., Rodríguez-Gómez, G., et al. (2019). The earliest cut marks of Europe: a discussion on hominin subsistence patterns in the Orce sites (Baza basin, SE Spain). *Sci. Rep.* 9, 1–13. doi: 10.1038/s41598-019-51957-5
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., et al. (2011). Trophic downgrading of planet earth. *Science* 333, 301–306. doi: 10.1126/SCIENCE.1205106/SUPPL_FILE/ESTES.SOM.PDF
- Estrada, G., and Marshall, A. (2024). Terrestriality across the primate order: A review and analysis of ground use in primates. *Evolutionary Anthropology: Issues News Rev.* 33. doi: 10.1002/evan.22032
- Falk, D., Redmond, J. C. Jr., Guyer, J., Conroy, C., Recheis, W., Weber, G. W., et al. (2000). Early hominid brain evolution: a new look at old endocasts. *J. Hum. Evol.* 38 (5), 695–717.
- Falótico, T., and Ottoni, E. (2023). Greater tool use diversity is associated with increased terrestriality in wild capuchin monkeys. *Am. J. Biol. Anthropol.* 181, 312–317. doi: 10.1002/ajpa.24740
- Fashing, P. J., Nguyen, N., Venkataraman, V. V., and Kerby, J. T. (2014). Gelada feeding ecology in an intact ecosystem at Guassa, Ethiopia: Variability over time and implications for theropithec and hominin dietary evolution. *Am. J. Phys. Anthropology* 155, 1–16. doi: 10.1002/AJPA.22559
- Feibel, C. S. (2011). A Geological History of the Turkana Basin. *Evol. Anthropol.: Issues, News, and Reviews* 20, 206–216. doi: 10.1002/evan.20331
- Feuerriegel, E. M., Green, D. J., Walker, C. S., Schmid, P., Hawks, J., Berger, L. R., et al. (2017). The upper limb of Homo naledi. *J. Hum. Evol.* 104, 155–173. doi: 10.1016/j.jhevol.2016.09.013
- Fleagle, J. (2013). *Primate adaptation and evolution* (Academic Press).
- Foley, R. (1993). “African terrestrial primates: the comparative evolutionary biology of Theropithecus and the Hominidae,” in *Theropithecus: The Rise and Fall of a Primate Genus* (Cambridge Univ. Press), 245–270.
- Foley, R. (2016). Mosaic evolution and the pattern of transitions in the hominin lineage. *Philos. Trans. R. Soc. B: Biol. Sci.* 371. doi: 10.1098/RSTB.2015.0244
- Foley, R. (2018). Evolutionary geography and the afrotropical model of hominin evolution. *BMSAP* 30, 17–31. doi: 10.13166/bmsap-2018-0001
- Foley, R., and Gamble, C. (2009). The ecology of social transitions in human evolution. *Philos. Trans. R. Soc. B: Biol. Sci.* 364, 3267–3279. doi: 10.1098/RSTB.2009.0136
- Fourvel, J. B., Thackeray, J. F., Brink, J. S., O'Regan, H., and Braga, J. (2018). Taphonomic interpretations of a new Plio-Pleistocene hominin-bearing assemblage at Kromdraai (Gauteng, South Africa). *Quaternary Sci. Rev.* 190, 81–97. doi: 10.1016/j.quascirev.2018.04.018
- Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E., and Arasa-Gisbert, R. (2019). Ecological traits of the world's primates. *Sci. Data* 6, 55. doi: 10.1038/s41597-019-0059-9
- Gathogo, P., and Brown, F. (2006). Stratigraphy of the Koobi Fora Formation (Pliocene and Pleistocene) in the Ileret region of northern Kenya. *J. Afr. Earth Sci.* 45, 369–390. doi: 10.1016/j.jafrearsci.2006.03.006
- Gaynor, K., Brown, J., Middleton, A., Power, M., and Brashares, J. (2019). Landscapes of fear: spatial patterns of risk perception and response. *Trends Ecol. Evol.* 34, 355–368. doi: 10.1016/j.tree.2019.01.004
- Georgiou, L., Dunmore, C. J., Bardo, A., Buck, L. T., Hublin, J. J., Pahr, D. H., et al. (2020). Evidence for habitual climbing in a Pleistocene hominin in South Africa. *Proc. Natl. Acad. Sci. United States America* 117, 8416–8423. doi: 10.1073/PNAS.1914481117
- Gilbert, C. C., Frost, S. R., Pugh, K. D., Anderson, M., and Delson, E. (2018). Evolution of the modern baboon (*Papio hamadryas*): A reassessment of the African Plio-Pleistocene record. *J. Hum. Evol.* 122, 38–69. doi: 10.1016/j.jhevol.2018.04.012
- Gommery, D., Pickford, M., and Senut, B. (2007). A case of carnivore-inflicted damage to a fossil femur from Swartkrans, comparable to that on a hominid femur representing Orrorin tugenensis, BAR 1003'00 (Kenya): scientific notes. *Ann. Transvaal Museum* 44, 215–218. Available online at: <https://hdl.handle.net/10520/EJC83650>.
- Grabowski, M., and Jungers, W. L. (2017). Evidence of a chimpanzee-sized ancestor of humans but a gibbon-sized ancestor of apes. *Nat. Commun.* 8, 1–10. doi: 10.1038/s41467-017-00997-4
- Green, D., Gordon, A., and Richmond, B. (2007). Limb-size proportions in Australopithecus afarensis and Australopithecus africanus. *J. Hum. Evol.* 52, 187–200. doi: 10.1016/j.jhevol.2006.09.001
- Gunz, P., Neubauer, S., Falk, D., Tafforeau, P., Le Cabec, A., Smith, T. M., et al. (2020). Australopithecus afarensis endocasts suggest ape-like brain organization and prolonged brain growth. *Sci. Adv.* 6. doi: 10.1126/SCIADV.AAZ4729/SUPPL_FILE/AAZ4729_SM.PDF
- Haeusler, M., and McHenry, H. M. (2004). Body proportions of Homo habilis reviewed. *J. Hum. Evol.* 46, 433–465. doi: 10.1016/j.jhevol.2004.01.004
- Haile-Selassie, Y. (2001). Late miocene hominids from the middle awash, Ethiopia. *Nature* 412, 178–181. doi: 10.1038/35084063
- Hamilton, W. J., Buskirk, R. E., and Buskirk, W. H. (1978). Environmental determinants of object manipulation by chacma baboons (*Papio ursinus*) in two southern African environments. *J. Hum. Evol.* 7, 205–216. doi: 10.1016/S0047-2484(78)80112-2
- Hammond, A. S., Alba, D. M., Almécija, S., and Moyà-Solà, S. (2013). Middle Miocene Pierolapithecus provides a first glimpse into early hominid pelvic morphology. *J. Hum. Evol.* 64, 658–666. doi: 10.1016/j.jhevol.2013.03.002
- Hammond, P., Gaynor, K. M., Easter, T., Biro, D., and Carvalho, S. (2025). Landscape-scale effects of season and predation risk on the terrestrial activity patterns of chacma baboons (*Papio ursinus*). *Am. J. Biol. Anthropol.* 186, e70052. doi: 10.1002/ajpa.70052
- Hammond, P., Lewis-Bevan, L., Biro, D., and Carvalho, S. (2022). Risk perception and terrestriality in primates: A quasi-experiment through habituation of chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique. *Am. J. Biol. Anthropol.* 179, 48–59. doi: 10.1002/AJPA.24567
- Hammond, A. S., Mavuso, S. S., Biernat, M., Braun, D. R., Jinnah, Z., Kuo, S., et al. (2021). New hominin remains and revised context from the earliest Homo erectus locality in East Turkana, Kenya. *Nat. Commun.* 12, 1–12. doi: 10.1038/s41467-021-22208-x
- Harcourt-Smith, W. (2010). The first hominins and the origins of bipedalism. *Evolution: Educ. Outreach* 3, 333–340. doi: 10.1007/s12052-010-0257-6
- Harcourt-Smith, W. (2016). Early hominin diversity and the emergence of the genus Homo. *J. Anthropol. Sci.* 94, 19–27. doi: 10.4436/jass.94035
- Harcourt-Smith, W., and Aiello, L. C. (2004). Fossils, feet and the evolution of human bipedal locomotion. *J. Anat.* 204, 403–416. doi: 10.1111/J.0021-8782.2004.00296.X
- Hart, D., and Sussman, R. W. (2011). “The influence of predation on primate and early human evolution: impetus for cooperation,” in *Origins Altruism Cooperation* (New York, NY: Springer New York), 19–40. doi: 10.1007/978-1-4419-9520-9_3
- Hatala, K. G., Roach, N. T., Behrensmeier, A. K., Falkingham, P. L., Gates, S. M., Williams-Hatala, E. M., et al. (2024). Footprint evidence for locomotor diversity and shared habitats among early Pleistocene hominins. *Sci. (New York N.Y.)* 386, 1004–1010. doi: 10.1126/SCIENCE.ADO5275/SUPPL_FILE/SCIENCE.ADO5275_CODES_S1_AND_S2.ZIP
- Hayward, M. W., and Slotow, R. (2009). Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South Afr. J. Wildlife Res.* 39, 109–125. doi: 10.10520/EJC117325
- Heldstab, S. A., Kosonen, Z. K., Koski, S. E., Burkart, J. M., Van Schaik, C. P., and Isler, K. (2016). Manipulation complexity in primates coevolved with brain size and terrestriality. *Sci. Rep.* 6, 1–9. doi: 10.1038/srep24528
- Herries, A. I. R., Martin, J. M., Leece, A. B., Adams, J. W., Boschian, G., Joannes-Boyau, R., et al. (2020). Contemporaneity of Australopithecus, Paranthropus, and early Homo erectus in South Africa. *Sci. (New York N.Y.)* 368. doi: 10.1126/SCIENCE.AAW7293
- Hill, K., Barton, M., and Magdalena Hurtado, A. (2009). The emergence of human uniqueness: Characters underlying behavioral modernity. *Evolutionary Anthropology* 18, 187–200. doi: 10.1002/EVAN.20224/FORMAT/PDF
- Hopwood, D. (2014). *Carnivorans as selective agents: Implications for the evolution of early Homo and Homo erectus behaviour* (Binghamton University).
- Hughes, J. K., Elton, S., and O'Regan, H. J. (2008). Theropithecus and ‘Out of africa’ dispersal in the plio-pleistocene. *J. Hum. Evol.* 54, 43–77. doi: 10.1016/j.jhevol.2007.06.004
- Hunt, K. D. (2016). Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. *J. Anat.* 228, 630–685. doi: 10.1111/JOA.12454
- Isbell, L. A., Bidner, L. R., Van Cleave, E. K., Matsumoto-Oda, A., and Crofoot, M. C. (2018). GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. *J. Hum. Evol.* 118, 1–13.
- Isbell, L. A., and Young, T. P. (1993). Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Anim. Behaviour* 45, 1233–1235. doi: 10.1006/anbe.1993.1145

- Ishida, H., and Pickford, M. (1997). A new Late Miocene hominoid from Kenya: *Samburupithecus kiptalami* gen. et sp. nov. *Comptes Rendus l'Académie Des. Sci. - Ser. IIA - Earth Planetary Sci.* 325, 823–829. doi: 10.1016/S1251-8050(97)82762-0
- Jablonski, N. (Ed.) (1993). *The Rise and Fall of a Primate Genus* (Cambridge University Press).
- Jablonski, N., Leakey, M. G., Ward, C. V., and Antón, M. (2008). *Koobi Fora research project, Vol. 6: The fossil monkeys* (California Academy of Sciences).
- Jolly, C. J. (2001). A proper study for mankind: Analogies from the Papionin monkeys and their implications for human evolution. *Am. J. Phys. Anthropology* 116, 177–204. doi: 10.1002/AJPA.10021
- Jungers, W. L., Larson, S. G., Harcourt-Smith, W., Morwood, M. J., Sutikna, T., Due Awe, R., et al. (2009). Descriptions of the lower limb skeleton of *Homo floresiensis*. *J. Hum. Evol.* 57, 538–554. doi: 10.1016/J.JHEVOL.2008.08.014
- Kappelman, J., Ketcham, R. A., Pearce, S., Todd, L., Akins, W., Colbert, M. W., et al. (2016). Perimortem fractures in Lucy suggest mortality from fall out of tall tree. *Nature* 537, 503–507. doi: 10.1038/nature19332
- Kim, P. S., McQueen, J. S., and Hawkes, K. (2019). Why does women's fertility end in mid-life? Grandmothering and age at last birth. *J. Theor. Biol.* 461, 84–91. doi: 10.1016/J.JTBI.2018.10.035
- Kimbel, W. H., and Deleuze, L. K. (2009). Lucy redux: A review of research on *Australopithecus afarensis*. *Am. J. Phys. Anthropology* 140, 2–48. doi: 10.1002/ajpa.21183
- Kivell, T. L. (2015). Evidence in hand: Recent discoveries and the early evolution of human manual manipulation. *Philos. Trans. R. Soc. B: Biol. Sci.* 370. doi: 10.1098/RSTB.2015.0105
- Kivell, T. L. (2019). Fossil ape hints at how walking on two feet evolved. *Nature* 575, 445–446. doi: 10.1038/d41586-019-03347-0
- Kivell, T. L., and Schmitt, D. (2009). Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. *Proc. Natl. Acad. Sci. United States America* 106, 14241–14246. doi: 10.1073/PNAS.0901280106
- Kramer, P. A. (2012). Brief communication: Could Kadanuumuu (KSD-VP-1/1) and Lucy (AL 288-1) have walked together comfortably? *Am. J. Phys. Anthropology* 149, 616–621. doi: 10.1002/AJPA.22169
- Kunimatsu, Y., Nakatsukasa, M., Sawada, Y., Sakai, T., Hyodo, M., Hyodo, H., et al. (2007). A new Late Miocene great ape from Kenya and its implications for the origins of African great apes and humans. *Proc. Natl. Acad. Sci. United States America* 104, 19220–19225. doi: 10.1073/PNAS.0706190104/SUPPL_FILE/06190FIG12.JPG
- Laidre, M. E. (2008). Spontaneous performance of wild baboons on three novel food-access puzzles. *Anim. Cogn.* 11, 223–230. doi: 10.1007/S10071-007-0104-5/TABLES/2
- Larson, S. G., Jungers, W. L., Tocheri, M. W., Orr, C. M., Morwood, M. J., Sutikna, T., et al. (2009). Descriptions of the upper limb skeleton of *Homo floresiensis*. *J. Hum. Evol.* 57, 555–570. doi: 10.1016/J.JHEVOL.2008.06.007
- Leakey, M., and Hay, R. (1979). Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. *Nature* 278, 317–323. doi: 10.1038/278317a0
- Lebatard, A. E., Boursell, D. L., Düringer, P., Jolivet, M., Braucher, R., Carcaillet, J., et al. (2008). Cosmogenic nuclide dating of *Sahelanthropus tchadensis* and *Australopithecus bahrelghazali*: Mio-Pliocene hominids from Chad. *Proc. Natl. Acad. Sci.* 105, 3226–3231. doi: 10.1073/PNAS.0708015105
- Lee-Thorp, J., Thackeray, J. F., and Van der Merwe, N. (2000). The hunters and the hunted revisited. *J. Hum. Evol.* 39, 565–576. doi: 10.1006/JHEV.2000.0436
- le Gros Clark, W. (1966). *History of the Primates: An Introduction to the Study of Fossil Man* (University of Chicago Press).
- Lepre, C. J., Roche, H., Kent, D. V., Harmand, S., Quinn, R. L., Brugal, J. P., et al. (2011). An earlier origin for the Acheulian. *Nature* 477, 82–85. doi: 10.1038/nature10372
- Levin, N. E. (2015). Environment and climate of early human evolution. *Annu. Rev. Earth Planetary Sci.* 43, 405–429. doi: 10.1146/ANNUREV-EARTH-060614-105310/1
- Lewis, M., and Werdelin, L. (2007). "Patterns of change in the Plio-Pleistocene carnivores of eastern Africa," in *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence* (Springer Netherlands), 77–105. doi: 10.1007/978-1-4020-3098-7_4
- Lin, B., Foxfoote, I. R., Miller, C. M., Venkatamaram, V., Kerby, J. T., Bechtold, E. K., et al. (2020). Leopard predation on gelada monkeys at Guassa, Ethiopia. *Wiley Online Library* 82. doi: 10.1002/ajp.23098
- Lovejoy, C. O., Suwa, G., Simpson, S. W., Matternes, J. H., and White, T. (2009a). The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. *Science* 326, 100–106. doi: 10.1126/SCIENCE.1175833/SUPPL_FILE/LOVEJOY1175833.SOM.PDF
- Lovejoy, C. O., Suwa, G., Simpson, S. W., Matternes, J. H., and White, T. D. (2009b). The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. *Science* 326, 100–106. doi: 10.1126/SCIENCE.1175833/SUPPL_FILE/LOVEJOY1175833.SOM.PDF
- Macchiarelli, R., Bergeret-Medina, A., Marchi, D., and Wood, B. (2020). Nature and relationships of *Sahelanthropus tchadensis*. *J. Hum. Evol.* 149, 102898. doi: 10.1016/J.JHEVOL.2020.102898
- MacLatchy, L. M., Cote, S. M., Deino, A. L., Kityo, R. M., Mugume, A. A. T., Rossie, J. B., et al. (2023). The evolution of hominoid locomotor versatility: Evidence from Moroto, a 21 Ma site in Uganda. *Science* 380. doi: 10.1126/SCIENCE.ABQ2835/SUPPL_FILE/SCIENCE.ABQ2835_MDAR_REPRODUCIBILITY_CHECKLIST.PDF
- Manthi, F. K., Cerling, T., Chrit, K. L., and Blumenthal, S. A. (2020). Diets of mammalian fossil fauna from Kanapoi, northwestern Kenya. *J. Hum. Evol.* 140, 102338. doi: 10.1016/j.jhevol.2017.05.005
- Margvelashvili, A., Tappen, M., Rightmire, G. P., Tsikaridze, N., and Lordkipanidze, D. (2022). An ancient cranium from Dmanisi: Evidence for interpersonal violence, disease, and possible predation by carnivores on Early Pleistocene *Homo*. *J. Hum. Evol.* 166, 103180. doi: 10.1016/J.JHEVOL.2022.103180
- Markham, A. C., Guttal, V., Alberts, S. C., and Altmann, J. (2013). When good neighbors don't need fences: Temporal landscape partitioning among baboon social groups. *Behav. Ecol. Sociobiology* 67, 875–884. doi: 10.1007/S00265-013-1510-0/TABLES/3
- Marsh, L. (2013). "Primates in fragments: ecology and conservation," in *Springer* (Springer Science & Business Media).
- Mauricio, A. (2013). *Sabertooth* (Indiana University Press).
- McBrearty, S., and Jablonski, N. (2005). First fossil chimpanzee. *Nature* 437, 105–108. doi: 10.1038/nature04008
- McCrossin, M. L., Benefit, B. R., Gitau, S. N., Palmer, A. K., and Blue, K. T. (1998). "Fossil evidence for the origins of terrestriality among old world higher primates," in *Primate Locomotion*. Eds. E. Strasser, J. G. Fleagle, A. L. Rosenberger and H. M. McHenry (Boston, MA: Springer) 353–396. doi: 10.1007/978-1-4899-0092-0_19
- McGraw, W. S., Cooke, C., and Shultz, S. (2006). Primate remains from African crowned eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Tai Forest: Implications for primate predation and early hominid taphonomy in South Africa. *Am. J. Phys. Anthropology* 131, 151–165. doi: 10.1002/ajpa.20420
- McNulty, K. P. (2010). Apes and tricksters: the evolution and diversification of humans' closest relatives. *Evolution: Educ. Outreach* 3, 322–332. doi: 10.1007/S12052-010-0251-Z/FIGURES/6
- McNutt, E. J., Hatala, K. G., Miller, C., Adams, J., Casana, J., Deane, A. S., et al. (2021). Footprint evidence of early hominid locomotor diversity at Laetoli, Tanzania. *Nature* 19, 1–4. doi: 10.1038/s41586-021-04187-7
- McNutt, E. J., Zipfel, B., and DeSilva, J. M. (2018). The evolution of the human foot. *Evolutionary Anthropology: Issues News Rev.* 27, 197–217. doi: 10.1002/EVAN.21713
- Meulman, E., Sanz, C. M., Visalberghi, E., and van Schaik, C. P. (2012). The role of terrestriality in promoting primate technology. *Evolutionary Anthropology: Issues News Rev.* 21, 58–68. doi: 10.1002/EVAN.21304
- Meulman, E., and van Schaik, C. (2013). "Orangutan tool use and the evolution of technology," in *Tool use in animals: Cognition and ecology* (Cambridge University Press), 176–202. doi: 10.1017/CBO9780511894800.011
- Meyer, M. R., Jung, J. P., Spear, J. K., Araiza, I. F., Galway-Witham, J., and Williams, S. A. (2023). Knuckle-walking in *Sahelanthropus*? Locomotor inferences from the ulnae of fossil hominins and other hominoids. *J. Hum. Evol.* 179, 103355. doi: 10.1016/J.JHEVOL.2023.103355
- Monte-Moreno, C. M., Crofoot, M. C., Grote, M. N., and Jansen, P. A. (2020). Increased terrestriality in a Neotropical primate living on islands with reduced predation risk. *J. Hum. Evol.* 143, 102768. doi: 10.1016/J.JHEVOL.2020.102768
- Moorjani, P., Amorim, C. E. G., Arndt, P. F., and Przeworski, M. (2016). Variation in the molecular clock of primates. *Natl. Acad. Sci.* 113, 10607–10612. doi: 10.1073/pnas.1600374113
- Mourthé, I. M. C., Guedes, D., Fidelis, J., Boubli, J. P., Mendes, S. L., and Strier, K. B. (2007). Ground use by northern muriquis (*Brachyteles hypoxanthus*). *Am. J. Primatology* 69, 706–712. doi: 10.1002/ajp.20405
- Moya-Solà, S., Köhler, M., Alba, D. M., Casanovas-Vilar, I., and Galindo, J. (2004). *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. *Science* 306, 1339–1344. doi: 10.1126/SCIENCE.1103094/ASSET/5AD3E600-C499-44E2-AA90-7E08C27046D1/ASSETS/GRAPHIC/306_1339_F6.JPG
- Negash, E. W., Alemseged, Z., Barr, W. A., Behrensmeyer, A. K., Blumenthal, S. A., Bobe, R., et al. (2024). Modern African ecosystems as landscape-scale analogues for reconstructing woody cover and early hominin environments. *J. Hum. Evol.* 197, 103604. doi: 10.1016/J.JHEVOL.2024.103604
- Negash, E., Wynn, J., and Bobe, R. (2019). *Woody Cover in Modern African Ecosystems: Implications for Hominin Landscape Dynamics* (The George Washington University).
- Nengo, I., Tafforeau, P., Gilbert, C. C., Fleagle, J. G., Miller, E. R., Feibel, C., et al. (2017). New infant cranium from the African Miocene sheds light on ape evolution. *Nature* 548, 169–174. doi: 10.1038/nature23456
- Neves, W., Valota, L., and Monteiro, C. (2024). Dental metrics of *Sahelanthropus tchadensis*: A comparative analysis with apes and Plio-Pleistocene hominins. *South Afr. J. Sci.* 120, 1–4. doi: 10.17159/SAJS.2024/16362
- Njau, J. K., and Blumenshine, R. J. (2012). Crocodylian and mammalian carnivore feeding traces on hominid fossils from FLK 22 and FLK NN 3, Plio-Pleistocene, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 63, 408–417. doi: 10.1016/J.JHEVOL.2011.05.008

- Nowak, K., le Roux, A., Richards, S. A., Scheijen, C. P. J., and Hill, R. A. (2014). Human observers impact habituated samango monkeys' perceived landscape of fear. *Behav. Ecol.* 25, 1199–1204. doi: 10.1093/beheco/aru110
- Ottoni, E. B., and Izar, P. (2008). Capuchin monkey tool use: Overview and implications. *Evolutionary Anthropology: Issues News Rev.* 17, 171–178. doi: 10.1002/EVAN.20185
- Palmer, M. S., Gaynor, K. M., Becker, J. A., Abraham, J. O., Mumma, M. A., and Pringle, R. M. (2022). Dynamic landscapes of fear: understanding spatiotemporal risk. *Trends Ecol. Evol.* 37, 911–925. doi: 10.1016/j.TREE.2022.06.007
- Palmqvist, P., Pérez-Claros, J. A., Janis, C. M., and Gröcke, D. R. (2008). Tracing the ecophysiology of ungulates and predator–prey relationships in an early Pleistocene large mammal community. *Palaeogeography Palaeoclimatology Palaeoecol.* 266, 95–111. doi: 10.1016/j.PALAEO.2008.03.015
- Pascual-Garrido, A., and Almeida-Warren, K. (2021). Archaeology of the perishable ecological constraints and cultural variants in chimpanzee termite fishing. *Curr. Anthropology* 62, 333–362. doi: 10.1086/713766/ASSET/IMAGES/LARGE/FG6.JPEG
- Patel, B. A., Susman, R. L., Rossie, J. B., and Hill, A. (2009). Terrestrial adaptations in the hands of *Equatorius africanus* revisited. *J. Hum. Evol.* 57, 763–772. doi: 10.1016/j.jhevol.2009.08.005
- Peppe, D. J., Cote, S. M., Deino, A. L., Fox, D. L., Kingston, J. D., Kinyanjui, R. N., et al. (2023). Oldest evidence of abundant C4 grasses and habitat heterogeneity in eastern Africa. *Science* 380, 173–177. doi: 10.1126/SCIENCE.ABQ2834
- Pickering, T., and Bunn, H. (2007). The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *J. Hum. Evol.* 53, 434–438. doi: 10.1016/j.jhevol.2007.01.012
- Pickering, T., Clarke, R. J., and Moggi-Cecchi, J. (2004). Role of carnivores in the accumulation of the Sterkfontein member 4 hominid assemblage: A taphonomic reassessment of the complete hominid fossil sample (1936–1999). *Am. J. Phys. Anthropology* 125, 1–15. doi: 10.1002/ajpa.10278
- Pickford, M., and Senut, B. (2004). Hominoid teeth with chimpanzee- and gorilla-like features from the Miocene of Kenya: implications for the chronology of ape-human divergence and biogeography of Miocene hominoids. *Anthropological Sci.* 113, 95–102. doi: 10.1537/ase.04S014
- Pobiner, B. L. (2020). “The zooarchaeology and paleoecology of early hominin scavenging,” in *Evolutionary Anthropology*, vol. 29. (Wiley-Liss Inc), 68–82. doi: 10.1002/evan.21824
- Potts, R. (2013). Hominin evolution in settings of strong environmental variability. *Quaternary Sci. Rev.* 73, 1–13. doi: 10.1016/j.QUASCIREV.2013.04.003
- Pozo-Montuy, G., Serio-Silva, J. C., and Bonilla-Sánchez, Y. M. (2011). Influence of the landscape matrix on the abundance of arboreal primates in fragmented landscapes. *Primates* 52, 139–147. doi: 10.1007/S10329-010-0231-5/TABLES/3
- Prabhat, A. M., Miller, C. K., Prang, T., Spear, J., Williams, S. A., and Desilva, J. M. (2021). Homoplasy in the evolution of modern human-like joint proportions in *Australopithecus afarensis*. *ELife* 10. doi: 10.7554/ELIFE.65897
- Prado-Martinez, J., Sudmant, P., Kidd, J., Li, H., Kelley, J., Lorente-Galdos, B., et al. (2013). Great ape genetic diversity and population history. *Nature* 499, 471–475. doi: 10.1038/nature12228
- Prang, T. (2019). The African ape-like foot of *Ardipithecus ramidus* and its implications for the origin of bipedalism. *ELife* 8. doi: 10.7554/ELIFE.44433
- Prang, T. (2022). New analyses of the *Ardipithecus ramidus* foot provide additional evidence of its African ape-like affinities: A reply to. *J. Hum. Evol.* 164, 103135. doi: 10.1016/j.jhevol.2021.103135
- Prang, T., Ramirez, K., Grabowski, M., and Williams, S. A. (2021). *Ardipithecus* hand provides evidence that humans and chimpanzees evolved from an ancestor with suspensory adaptations. *Sci. Adv.* 7, eabf2474. doi: 10.1126/sciadv.abf2474
- Presnyakova, D., Braun, D. R., Conard, N. J., Feibel, C., Harris, J. W. K., Pop, C. M., et al. (2018). Site fragmentation, hominin mobility and LCT variability reflected in the early Acheulean record of the Okote Member, at Koobi Fora, Kenya. *J. Hum. Evol.* 125, 159–180. doi: 10.1016/j.jhevol.2018.07.008
- Quinn, R., Lepre, C., Feibel, C., Wright, J., Mortlock, R., Harmand, S., et al. (2013). Pedogenic carbonate stable isotopic evidence for wooded habitat preference of early Pleistocene tool makers in the Turkana Basin. *J. Hum. Evol.* 65, 65–78. doi: 10.1016/j.jhevol.2013.04.002
- Raichlen, D. A., Pontzer, H., and Sockol, M. D. (2008). The Laetoli footprints and early hominin locomotor kinematics. *J. Hum. Evol.* 54, 112–117. doi: 10.1016/j.jhevol.2007.07.005
- Richmond, B., Begun, D., and Strait, D. (2001). Origin of human bipedalism: The knuckle-walking hypothesis revisited. *Am. J. Phys. Anthropology* 116, 70–105. doi: 10.1002/ajpa.10019
- Richmond, B., Green, D., Lague, M., Chirchir, H., Behrensmeyer, A., Bobe, R., et al. (2020). The upper limb of *Paranthropus boisei* from Ilkeret, Kenya. *J. Hum. Evol.* 141, 102727. doi: 10.1016/j.jhevol.2019.102727
- Richmond, B., and Jungers, W. (2008). Orrorin tugenensis femoral morphology and the evolution of hominin bipedalism. *Science* 319, 1662–1665. doi: 10.1126/SCIENCE.1154197/SUPPL_FILE/RICHMOND.SOM.PDF
- Richmond, B., and Strait, D. (2000). Evidence that humans evolved from a knuckle-walking ancestor. *Nature* 404, 382–385. doi: 10.1038/35006045
- Ripple, W., and Van Valkenburgh, B. (2010). Linking top-down forces to the Pleistocene megafaunal extinctions. *BioScience* 60, 516–526. doi: 10.1525/bio.2010.60.7.7
- Rizal, Y., Westaway, K. E., Zaim, Y., van den Bergh, G. D., Bettis, E. A., Morwood, M. J., et al. (2019). Last appearance of *Homo erectus* at Ngandong, Java, 117,000–108,000 years ago. *Nature* 577, 381–385. doi: 10.1038/s41586-019-1863-2
- Rogers, M., Harris, J., and Feibel, C. (1994). Changing patterns of land use by Plio-Pleistocene hominids in the Lake Turkana Basin. *J. Hum. Evol.* 27, 139–158. doi: 10.1006/jhev.1994.1039
- Ruff, C. (2009). Relative limb strength and locomotion in *Homo habilis*. *Am. J. Phys. Anthropology* 138, 90–100. doi: 10.1002/AJPA.20907
- Samuni, L., Lemieux, D., Lamb, A., Galdino, D., and Surbeck, M. (2022). Tool use behavior in three wild bonobo communities at Kokolopori. *Am. J. Primatology* 84, e23342. doi: 10.1002/AJP.23342
- Sayers, K., Raghanti, M. A., and Lovejoy, C. O. (2012). Human evolution and the chimpanzee referential doctrine. *Annual Rev. Anthropol.* 41, 119–138. doi: 10.1146/ANNUREV-ANTHRO-092611-145815
- Schuster, M., Düringer, P., Ghienne, J. F., Roquin, C., Sepulchre, P., Moussa, A., et al. (2009). Chad basin: paleoenvironments of the sahara since the late miocene. *Comptes Rendus Geosci.* 341, 603–611. doi: 10.1016/j.CRTE.2009.04.001
- Schuster, M., Düringer, P., Ghienne, J. F., Vignaud, P., Mackaye, H. T., Likius, A., et al. (2006). The age of the Sahara desert. *Sci. (New York N.Y.)* 311, 821. doi: 10.1126/SCIENCE.1120161
- Searle, C. E., Smit, J. B., Cusack, J. J., Strampelli, P., Grau, A., Mkuburo, L., et al. (2021). Temporal partitioning and spatiotemporal avoidance among large carnivores in a human-impacted African landscape. *PloS One* 16, e0256876. doi: 10.1371/JOURNAL.PONE.0256876
- Semaw, S., Simpson, S. W., Quade, J., Renne, P. R., Butter, R. F., McIntosh, W. C., et al. (2005). Early pliocene hominids from gona, Ethiopia. *Nature* 433, 301–305. doi: 10.1038/nature03177
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., and Coppens, Y. (2001). First hominid from the miocene (Lukole formation, Kenya). *Comptes Rendus l'Académie Des. Sci. - Ser. IIA - Earth Planetary Sci.* 332, 137–144. doi: 10.1016/S1251-8050(01)01529-4
- Senut, B., Pickford, M., Gommery, D., and Ségalen, L. (2018). Palaeoenvironments and the origin of hominid bipedalism. *Historical Biol.* 30, 284–296. doi: 10.1080/08912963.2017.1286337
- Senut, B., and Tardieu, C. (1985). “Functional aspects of Plio-Pleistocene hominid limb bones: implications for taxonomy and phylogeny,” in *Ancestors: the hard evidence*. Ed. A. Liss, 193–201. Available online at: <https://cir.nii.ac.jp/crid/1572824499682102016>
- Shipman, P. (1986). Scavenging or hunting in early hominids: theoretical framework and tests. *Am. Anthropologist* 88, 27–43. doi: 10.1525/AA.1986.88.1.02A00020
- Smith, T. M., Tafforeau, P., Pouech, J., and Begun, D. R. (2019). Enamel thickness and dental development in *Rudapithecus hungaricus*. *J. Hum. Evol.* 136, 102649. doi: 10.1016/j.jhevol.2019.102649
- Sponheimer, M., Alemseged, Z., Cerling, T., Grine, F., Kimbel, W., Leakey, M., et al. (2013). Isotopic evidence of early hominin diets. *Proc. Natl. Acad. Sci.* 110, 10513–10518. doi: 10.1073/pnas.1222579110
- Spoor, F., Gunz, P., Neubauer, S., Stelzer, S., Scott, N., Kwekason, A., et al. (2015). Reconstructed *Homo habilis* type OH 7 suggests deep-rooted species diversity in early *Homo*. *Nature* 519, 83–86. doi: 10.1038/nature14224
- Stamos, P. A., and Alemseged, Z. (2023). Hominin locomotion and evolution in the Late Miocene to Late Pliocene. *J. Hum. Evol.* 178, 103332. doi: 10.1016/j.jhevol.2023.103332
- Stern, J. T., and Susman, R. L. (1983). The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropology* 60, 279–317. doi: 10.1002/AJPA.1330600302
- Stringer, C. (2002). Modern human origins: progress and prospects. *Philos. Trans. R. Soc. London. Ser. B: Biol. Sci.* 357, 563–579. doi: 10.1098/RSTB.2001.1057
- Strum, S., and Mitchell, W. (1987). “Baboon models and muddles,” in *The evolution of human behaviour: Primate models* (SUNY Press). 87–104.
- Suwa, G., Kono, R. T., Katoh, S., Asfaw, B., and Beyene, Y. (2007). A new species of great ape from the late Miocene epoch in Ethiopia. *Nature* 448, 921–924. doi: 10.1038/nature06113
- Swedell, L., Plummer, T., Swedell, L., and Plummer, T. (2012). A papionin multilevel society as a model for hominin social evolution. *Int. J. Primatology* 33, 1165–1193. doi: 10.1007/S10764-012-9600-9
- Tabacow, F. P., Mendes, S. L., and Strier, K. B. (2009). Spread of a terrestrial tradition in an arboreal primate. *Am. Anthropologist* 111, 238–249. doi: 10.1111/J.1548-1433.2009.01116.X
- Takemoto, H. (2004). Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *Am. J. Phys. Anthropology* 124, 81–92. doi: 10.1002/ajpa.10342
- Terborgh, J., Lopez, L., Nuñez, P. V., Rao, M., Shahabuddin, G., Orihuela, G., et al. (2001). Ecological meltdown in predator-free forest fragments. *Science* 294, 1923–1926. doi: 10.1126/SCIENCE.1064397

- Thompson, J., Carvalho, S., Marean, C., and Alemseged, Z. (2019). Origins of the human predatory pattern the transition to large-animal exploitation by early hominins. *Ora.Ox.Ac.Uk* 60, 1–23. doi: 10.1086/701477
- Thorpe, S. K., Holder, R. L., and Crompton, R. H. (2007). Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* 316, 1328–1331. doi: 10.1126/science.1140799
- Tomasello, M., and Vaish, A. (2013). Origins of human cooperation and morality. *Annual Rev. Psychol.* 64, 231–255. doi: 10.1146/ANNUREV-PSYCH-113011-143812
- Uno, K. T., Polissar, P. J., Jackson, K. E., and Demenocal, P. B. (2016). Neogene biomarker record of vegetation change in eastern Africa. *Proc. Natl. Acad. Sci. United States America* 113, 6355–6363. doi: 10.1073/PNAS.1521267113/SUPPL_FILE/PNAS.1521267113.SD07.XLSX
- Urciuoli, A., and Alba, D. M. (2023). Systematics of Miocene apes: State of the art of a neverending controversy. *J. Hum. Evol.* 175, 103309. doi: 10.1016/j.jhevol.2022.103309
- Val, A., Taru, P., and Steininger, C. (2014). New taphonomic analysis of large-bodied primate assemblage from Cooper's D, Bloubank Valley, South Africa. *South Afr. Archaeological Bull.* 69, 49–58. Available online at: <http://www.jstor.org/stable/24332730>.
- Van Valkenburgh, B., Hayward, M. W., Ripple, W. J., Meloro, C., and Roth, V. L. (2016). The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proc. Natl. Acad. Sci. United States America* 113, 862–867. doi: 10.1073/PNAS.1502554112
- Villmoare, B., Kimbel, W. H., Seyoum, C., Campisano, C. J., DiMaggio, E. N., Rowan, J., et al. (2015). Early Homo at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science* 347, 1352–1355.
- Visalberghi, E., Sirianni, G., Fragaszy, D., and Boesch, C. (2015). Percussive tool use by Tai Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: a comparison. *Philos. Trans. R. Soc. B: Biol. Sci.* 370. doi: 10.1098/RSTB.2014.0351
- Vrba, E., Denton, G., and Prentice, M. (1989). Climatic influences on early hominid. *Ossa* 14, 127–156.
- Ward, C. (2002). Interpreting the posture and locomotion of Australopithecus afarensis: Where do we stand? *Am. J. Phys. Anthropology* 119, 185–215. doi: 10.1002/AJPA.10185
- Ward, C. V., Hammond, A. S., Plavcan, J. M., and Begun, D. R. (2019). A late Miocene hominid partial pelvis from Hungary. *J. Hum. Evol.* 136, 102645. doi: 10.1016/j.jhevol.2019.102645
- Ward, C., Kimbel, W., and Johanson, D. (2011). Complete fourth metatarsal and arches in the foot of Australopithecus afarensis. *Sci. (New York N.Y.)* 331, 750–753. doi: 10.1126/SCIENCE.1201463
- Ward, C., Leakey, M., and Walker, A. (1999). The new hominid species Australopithecus anamensis. *Evolutionary Anthropology: Issues News Rev.* 7, 197–205. doi: 10.1002/(SICI)1520-6505(1999)7:6<3C197::AID-EVAN4%3E3.0.CO;2-T
- Ward, C. V., Leakey, M. G., and Walker, A. (2001). Morphology of australopithecus anamensis from kanapoi and allia bay, Kenya. *J. Hum. Evol.* 41, 255–368. doi: 10.1006/jhev.2001.0507
- Washburn, S. (1960). Tools and human evolution. *Sci. Am.* 203, 63–75. doi: 10.1038/scientificamerican0960-62
- Werdelin, L., and Lewis, M. (2005). Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. *Zoological J. Linn. Soc.* 144, 121–144. doi: 10.1111/j.1096-3642.2005.00165.x
- Werdelin, L., and Lewis, M. (2013a). *Koobi fora research project volume 7: The Carnivora* (California Academy of Sciences).
- Werdelin, L., and Lewis, M. (2013b). Temporal change in functional richness and evenness in the eastern african plio-pleistocene carnivoran guild. *PLoS One* 8, e57944. doi: 10.1371/journal.pone.0057944
- White, T., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C., Suwa, G., et al. (2009). Ardipithecus ramidus and the paleobiology of early hominids. *Science* 326, 64–86. doi: 10.1126/science.1175802
- White, T., Lovejoy, C. O., Asfaw, B., Carlson, J. P., and Suwa, G. (2015). Neither chimpanzee nor human, Ardipithecus reveals the surprising ancestry of both. *Proc. Natl. Acad. Sci. United States America* 112, 4877–4884. doi: 10.1073/PNAS.1403659111/-/DCSUPPLEMENTAL
- White, T., WoldeGabriel, G., Asfaw, B., Ambrose, S., Beyene, Y., Bernor, R., et al. (2006). Asa issie, aramis and the origin of australopithecus. *Nature* 440, 883–889. doi: 10.1038/nature04629
- Wilkinson, R. D., Steiper, M. E., Soligo, C., Martin, R. D., Yang, Z., and Tavaré, S. (2011). Dating primate divergences through an integrated analysis of palaeontological and molecular data. *Systematic Biol.* 60, 16–31. doi: 10.1093/sysbio/syq054
- Willems, E. P., and Van Schaik, C. P. (2017). The social organization of Homo ergaster: Inferences from anti-predator responses in extant primates. *J. Hum. Evol.* 109, 11–21. doi: 10.1016/j.jhevol.2017.05.003
- Williams, S. A., Prang, T., Meyer, M. R., Nalley, T. K., van der Merwe, R., Yelverton, C., et al. (2021). New fossils of Australopithecus sediba reveal a nearly complete lower back. *ELife* 10. doi: 10.7554/ELIFE.70447
- Williams, S. A., Prang, T., Meyer, M. R., Russo, G. A., and Shapiro, L. J. (2020). Reevaluating bipedalism in danuvius. *Nature* 586, E1–E3. doi: 10.1038/s41586-020-2736-4
- Williams, S. A., Prang, T. C., Russo, G. A., Young, N. M., and Gebo, D. L. (2023). African apes and the evolutionary history of orthograde and bipedalism. *Am. J. Biol. Anthropology* 181, 58–80. doi: 10.1002/AJPA.24684
- Woldegabriel, G., White, T. D., Suwa, G., Renne, P., de Heinzelin, J., Har, W., et al. (1994). Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature* 371, 330–333. doi: 10.1038/371330a0
- Wood, B., and Boyle, E. (2016). Hominin taxic diversity: Fact or fantasy? *Am. J. Phys. Anthropology* 159, S37–S78. doi: 10.1002/ajpa.22902
- Wood, B., and Collard, M. (1999). The human genus. *Science* 284, 65–71. doi: 10.1126/SCIENCE.284.5411.65/ASSET/EA39798D-9B38-4769-B655-8F0212F2EB46/ASSETS/GRAPHIC/SE0797267002.JPEG
- Wright, K. A., Biondi, L., Visalberghi, E., Ma, Z., Izar, P., and Fragaszy, D. (2019). Positional behavior and substrate use in wild adult bearded capuchin monkeys (Sapajus libidinosus). *Am. J. Primatology* 81, e23067. doi: 10.1002/AJP.23067
- Wynn, J. G., Alemseged, Z., Bobe, R., Grine, F. E., Negash, E. W., and Sponheimer, M. (2020). Isotopic evidence for the timing of the dietary shift toward C4 foods in eastern African Paranthropus. *Proc. Natl. Acad. Sci. United States America* 117, 21978–21984. doi: 10.1073/PNAS.2006221117/-/DCSUPPLEMENTAL
- Zollikofer, C. P. E., Ponce De León, M. S., Lieberman, D. E., Guy, F., Pilbeam, D., Likies, A., et al. (2005). Virtual cranial reconstruction of Sahelanthropus tchadensis. *Nature* 434, 755–759. doi: 10.1038/nature03397