Author's Accepted Manuscript: Roberts, P., Boivin, N., Lee-Thorp. J., Petraglia, M., Stock, J.T. (2016) Tropical forests and human evolution. *Evolutionary Anthropology* 25(6):306-317. DOI: 10.1002/evan.21508

Tropical forests and the genus *Homo*

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This manuscript includes:
37 double-spaced text pages including references and figure captions
4 Figures
0 Tables

Key words: Tropics, rainforest, ape, hominin, Anthropocene

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Tropical forests constitute some of the most diverse, complex, but also threatened, terrestrial ecosystems on the planet. They provide crucial ecosystem services (e.g. foods, construction materials, and medicinal resources) for vast portions of the world's human population. These environments provided the cradle for the emergence of early hominins in Africa as well as a habitat for the continued survival of our closest living relatives, the great apes. However, while the important early role of tropical forests in human evolution has been recognized, forest adaptations tend to be eclipsed in later evolutionary narratives, including the emergence of the genus *Homo* and the expansion of *Homo* species across the globe. While researchers have argued for Early-Middle Pleistocene evidence for potential tropical forest occupation by our genus in Southeast Asia, it is only with the emergence of *Homo sapiens* that a *Homo* species can definitively be seen engaging, and even specializing, in the use of tropical forests at an ever-intensifying rate. Indeed, it is only our species, via the medium of activities such as farming, trade networks, complex states, and industrial exploitation, that has affected tropical forests on scales that threaten their very existence.

Tropical forests are some of the oldest land-based ecosystems on the planet and contain over half of the world's existing plant and animal species (Wilson 1988; Whitmore 1998). This inherent diversity, the regular supply of fresh water from well-fed streams or rivers, and a lack of high amplitude swings in resource availability likely contributed to the important role these environments played in the origins of all the great apes, including hominins, during the Miocene (Tuttle, 2014). Today these habitats also provide the settings for significant biological diversity among our closest living relatives, the African great apes (Tuttle, 2014). Despite their ecological richness, the role of these habitats in Plio-Pleistocene hominin diversity, the appearance of our genus (*Homo*), and its movement into Eurasia, remains less clear. Mosaics of open, mixed woodland and forest habitats in eastern and southern Africa have received the most attention in these processes on the basis of palaeoecological and palaeodietary reconstruction, including stable isotope analysis. (Sponheimer et al., 2013). From this point, until the emergence of our species *Homo sapiens* (Roberts and Petraglia, 2015), evidence for tropical forest use appears remarkably scarce.

We review the dynamic relationship between our genus and tropical forests, one of the most over-utilized environments on the globe today. We begin by briefly contrasting evidence for forest occupation amongst some of the earliest members of the hominin clade with evidence for an increasing emphasis on C_4 resources and open environments among Pliocene and Pleistocene hominin species, including the earliest members of the genus *Homo*, in Africa. We then evaluate the extent to which this apparent 'gap' in tropical forest use is real through analysis of evidence for the palaeoecological context for some of the earliest fossils of our genus in Southeast Asia. This region is crucial in the assessment of early tropical forest exploitation by our genus not only because it has it yielded some of the earliest *Homo* fossils beyond Africa, but also because it is covered by vast swathes of tropical forest today. We compare this evidence to that for the global relationship between the only remaining species of *Homo*, *Homo sapiens*, and tropical forests, and its culmination in increasingly large-scale forest ecosystem impacts.

Tropical forests and opportunities for hominin existence

We define tropical forests as those forest formations that lie between the Tropic of Cancer (23°26′14.0″N) and the Tropic of Capricorn (23°26′14.0″S) (**Figure 1**). The term 'tropical forest' is most often associated with tropical rainforests, a designation first employed by the botanist A.F.W. Schimper in 1898 (*tropische Regenwald*) (Allaby, 2010). While ecologists have defined tropical rainforests on the basis of their unique plant species composition (White, 1983), high precipitation (Grainger, 1996), and temperature (e.g. mean annual temperature >24°C) (Holdridge, 1947), the key climatic parameter is low seasonality of both temperature and rainfall (Whitmore, 1998). Rainforests develop when every month is wet (with 100 mm rainfall or more), or where there are only short, dry spells lasting just a few days or weeks. This consistency in warm temperature and high humidity has been argued to be crucial for the diversity of rainforest biota (Whitmore, 1998), although high species diversity has also been linked to the sheltering of biodiversity in forest refugia during dry, glacial periods, that then expands as climate ameliorates (Haffer, 1969; Hamilton, 1972) (**Box 1**).

These climatic parameters, as well as local factors such as geological substrate, altitude, and precipitation dynamics, lead to a series of different tropical forest formations, including semi-evergreen rainforest, montane rainforest, heath forest, peat swamp forest, freshwater swamp forest and dry deciduous forests, whose frequency differs across the Americas, Africa, and Asia (Whitmore, 1998) (**Figure 1**). Where seasonality and dry periods of more than two months exist in the tropics, monsoonal forests, deciduous forests, open forest structures, and mosaics prevail (Grainger, 1996). Each of these forest types presents different challenges and opportunities for hominin communities (**Box 1**). For example, while the masting dipterocarp trees of evergreen tropical forests in Southeast Asia provide an abundance of fruit for local primate, and potentially hominin, populations (Knott, 1998), high frequencies of acidic peat swamp and heath forest soils often prohibit the growth of crops (Whitmore, 1998). Similarly, the formation of deciduous, open forest structures and grassland mosaics along the borders of African rainforests would have presented important, simultaneous opportunities of forest resources and fauna and access to large game populations (Blome et al., 2012) (**Box 1**).

There is also considerable diversity *within* a given tropical forest formation, structured by verticality. Forests are frequently divided into different strata, with vegetation and resources conceptualized as a series of vertically stratified layers, from ground level to the canopy that each present different resources for hominin communities (**Figure 2**) (Denslow, 1987). In dense forests, low light on the forest floor can lead to a paucity of vegetation and fauna. By contrast, tree fruits and lianas in canopy and emergent canopy layers often provide food for large numbers of primates, birds, and insects that can all be used as sources of food (Whitmore, 1998) (**Figure 2**). Canopy gaps can also occur within forests, as a result of the presence of tree death or the intersection of streams and rivers. Gaps at ground level are rapidly colonized by seedlings and often facilitate increased species-richness and higher densities of vegetation growth (Denslow, 1987). Large numbers of fauna gather in these locations to exploit this richness and, in the case of streams and rivers, to drink (**Figure 2**). Given the reliable access to water, ease of navigation, and relative faunal and floral richness it is possible that tropical forest canopy gaps around rivers provided crucial corridors for the expansion of hominins and, later, farming communities in the past (Grollemund et al., 2014).

Box 1: Forests in flux

The equatorial portions of Africa and beyond have generally been considered as relatively stable, and hence little-considered in climate-linked models of hominin and human evolution (Basell, 2008). The assumed stability of these environments is not supported, however, by hard evidence for considerable changes in the extent, structure, and composition of tropical forests on a number of different temporal and spatial scales, from the Miocene to the Holocene. Under low CO_2 conditions C_3 plants, which dominate tropical and sub-tropical forest ecologies, lose their adaptive advantage to C_4 grasses, resulting in forest retreat (Jolly and Haxeltine, 1997; Morley, 2001). Similarly, decreased temperature and precipitation causes forest fragmentation and re-structuring particularly at high altitudes or sub-tropical fringes (Jolly and Haxeltine, 1997; Mayle et al., 2004). Changing seasonality in rainfall and temperature, although difficult to measure, will also have had considerable impacts on regional tropical forest extent and composition (Whitmore, 1998).

Past changes in rainfall, temperature, and climatic seasonality, have strongly regional impacts on tropical forests (Malhi and Wright, 2011). The tropical rainforests of Africa have been argued to be particularly vulnerable to climate-linked changes in extent and structure (Morley, 2001; Malhi and Wright, 2011). Here, faunal abundance records and stable isotope analysis of fossil fauna (Reed, 1997; Uno et al., 2011) have been used to postulate an expansion of C_4 grasses and savanna vegetation, at the expense of these formerly extensive forests (Uno et al., 2011), during the Pliocene and Pleistocene epochs. These changes have been considered advantageous to broad-spectrum hominin foragers (**Box 2**), adaptive radiation concomitant with changes in community structure, and the eventual emergence of the genus *Homo* (Potts, 1998; de Menocal, 2004). Similarly, the expansion of *Homo sapiens* in tropical Africa has been linked to forest fragmentation during colder and drier glacial periods when mosaic forest-grassland environments became available (Basell, 2008; Blome et al., 2012).

In contrast to Africa, the extent and structure of the tropical forests of Southeast Asia and the Americas are more stable (Mayle and Bush, 2011), perhaps necessitating rapid adaptations to tropical forests by hominin and human populations entering these regions (Semah et al., 2009; Bush et al., 2011). For example, in Southeast Asia the migration of *Homo erectus* in the region *c.* 1.5 Ma has been argued to represent the earliest encounters of our genus with tropical forest exploitation (Semah et al., 2009; Semah and Semah, 2012; Semah et al., 2016). Similarly, some of the earliest *Homo sapiens* fossils in Asia are associated with the intensive use of a tropical forest environment in Borneo, Southeast Asia (Barker et al., 2007). That said, others have highlighted the distinctive, important impacts of changes in sea-level and associated land-mass fragmentation in promoting forest-grassland mosaics that facilitated the expansion of *Homo erectus* (Bettis et al., 2009; Ciochon, 2009; Marwick, 2009) and *Homo sapiens* (Bird et al., 2005) throughout this region.

Climate fluctuations across the LGM, Terminal Pleistocene-Holocene boundary, and the Holocene have also been argued to have regionally-varied impacts on the ever-intensifying relationship between humans and tropical forests at this time. Tropical experimentations with agriculture in Melanesia at Kuk Swamp appear to be associated with altitudinal gradients from lowland to montane tropical forests that would be particularly vulnerable to reductions in temperature, lower atmospheric CO_2, and declines in precipitation across the Pleistocene-Holocene transition (Golson, 1989; Denham et al., 2009). The early onset of forest burning in this region, and intensifying burning across the Terminal Holocene boundary, may represent active human attempts to maintain these ecotonal boundaries and preserve resource diversity (Golson, 1989; Denham *et al.*, 2004; Haberle *et al.*, 2012). The origins of agricultural experimentation in the Americas also appear to be associated with seasonal types of lowland tropical forest and mid-elevation moist forest habitats (Piperno 2011).

A shady cradle

The rich, but variable, opportunities presented by tropical forests have provided an important catalyst for the evolution of significant dietary and locomotor diversity in our closest living relatives, the great apes. The most arboreal of the great apes, the orangutan (*Pongo pygmaeus*), employs bipedal locomotion most frequently. It has been argued that this behavior is an adaptation to the navigation of thin, flexible branches when gathering fruit high in the canopy (Thorpe *et al.*, 2007). The focus on these fruits likely represents an adaptation to the characteristic masting dipterocarp trees found in the evergreen rainforests of Southeast Asia (Knott, 1998). Chimpanzees (*Pan troglodytes*) demonstrate large dietary variability across the tropical forests of Africa. In the evergreen and semi-evergreen rainforests of the West African lowlands, chimpanzees congregate in large groups to eat ripe fruit when it is available during the wet season, but fragment into smaller groups and consume a variety of other lower quality foods during the dry season (Tutin et al., 1991). Furthermore, chimpanzees inhabiting the drier, mosaic forests of Fongoli, Senegal have been documented using tool-assisted hunting to obtain the meat of small mammals (Pruetz and Bertolani, 2007). While foraging, chimpanzees will regularly demonstrate bipedal forms of locomotion across the tropical forest floor (Crompton et al., 2010).

It is therefore perhaps not surprising that the origin of the hominin clade, and most likely also the Last Common Ancestor of great apes and humans, is to be found within tropical forest settings in Africa. The ubiquity of facultative bipedalism, combined with other locomotor patterns among extant apes, suggests that the earliest members of the hominin clade evolved habitual bipedalism while retaining other forms of locomotion, some of which are relevant in forest/closed environments. For example, the femur of *Orrorin tugenensis* (6.1-5.7 Ma) has a long, antero-posteriorly narrow neck and a wide proximal diaphysis, features shared with later bipedal australopithecines (Richmond and Jungers, 2008), while muscle insertions on the humerus and the curvature of phalanges have been linked to tree climbing (Senut et al., 2001). Similarly, the lower limb proportions and the foot and hand morphology of *Ardipithecus ramidus* (*c.* 4.4 Ma) have been associated with tree climbing, while its pelvic morphology has been linked to ground-based bipedal walking (White et al., 2009; Kimbel et al., 2014).

The period between *c.* 4 and 2 Ma provides evidence for an adaptive radiation of habitual and obligate bipedal species within the hominin clade. However, arboreal-like faculties persist even as the accumulation of evidence for habitual terrestrial locomotion continues, perhaps hinting at the ongoing importance of arboreal subsistence within open grassland/tropical forest mosaics in Africa during the Pliocene and Pleistocene (**Box 1**). Highly-derived pelvic morphology, a valgus angle of the femur, and derived foot morphology have been interpreted as evidence for increasing bipedal specialization in *Australopithecus afarensis* (*c.* 3.9-2.9 Ma) (Latimer and Lovejoy, 1989). However, the limb and scapular morphology and ontogeny of *Australopithecus afarensis* has suggested that their locomotor repertoire included a substantial amount of climbing (Green and Alemseged, 2012). A similar mosaic is seen in *Australopithecus sediba* (1.97 Ma) (Kivell et al., 2011). Even in the context of our genus biomechanical analyses of the limb bones of *Homo habilis* also demonstrate high humeral relative to femoral strength, which suggests at least partial arboreality among *Homo habilis* relative to *Homo erectus*, with the more derived pattern not evolving until after 1.6 Mya (Ruff, 2009).

Nevertheless, between 4 and 2 Ma researchers have placed most emphasis on the new opportunities afforded by expanding open grassland environments and C_4 resources in the evolution of specialized bipedalism and tool use (Uno et al., 2011) (**Box 1**). By 2 Ma, with more human-like thumb-to-finger proportions and spinal orientation, *Paranthropus boisei, Paranthropus robustus*, *Australopithecus africanus* and early putative members of the genus *Homo* appear to have specialized adaptations to upright walking and ground movement (Skinner et al., 2015). Phenotypic variability among early *Homo* species also appears to have been driven by thermal stress within the Turkana Basin (Will and Stock, 2015). Likewise, stable isotopic dietary information from multiple hominin species points to increasing engagement with foods originating in ^{13}C-enriched C_4 grasses or sedges after *c.* 4 Ma (**Figure 3**). Focus on C_3 resources, likely linked to woodland or forest habitats, in earlier hominin species, *Ardipithecus ramidus* and *Australopithecus anamensis*, gives way to increasing engagement with C_4 resources in *Australopithecus afarensis*, *Australopithecus africanus*, *Paranthropus boisei* and *Homo* (**Figure 3**). This period has therefore been seen as possibly representing the onset of a lacuna in evidence for hominin tropical forest use until the evolution of our species, *Homo sapiens*, 200 ka. However, this lacuna may be one of research focus and preservation rather than real hominin preference (**Box 2**).

Box 2. Forests of plenty or green deserts?

In the 1980s and 1990s it was postulated that a scarcity of fat- and protein-rich fauna, and carbohydrate-rich plants (Hart and Hart, 1986), meant that dedicated human rainforest foraging in these ‘green deserts’ was impossible without recourse to other environments and resources, with many tropical forest foragers apparently trading with agricultural communities in order to meet their subsistence needs (Bailey et al., 1989). This hypothesis was criticized by researchers who showed that tropical game can be fat-rich, that many other carbohydrate-rich animal and plant resources exist in tropical forests including honey and palm starch, and that underground storage organs are in fact relatively prevalent in some tropical forests (Bahuchet et al., 1991; Brosius, 1991; Dentan, 1991). In the ethnographic literature, specialized tropical forest foraging completely independent of agriculture has been definitively demonstrated (Hewlett, 2014).

This literature has, however, taken time to filter into studies of the past. Tropical forests are often perceived as barriers to hominin population movement, with studies citing difficulties of navigation, thermoregulation, limited large game opportunities and a lack of easily-processed foods, as well as the need for savannah-adapted humans to develop the technologies and expertise necessary to expand into forest environments (Bird et al., 2005; Dennell and Roebroeks, 2005; Cosgrove et al., 2007; Boivin et al., 2013). This has not been helped by poor archaeological visibility in tropical forests as a result of poor archaeological preservation, including the rapid disintegration of organic remains (Tappen, 1994), and also difficulties of archaeological survey in these environments until the recent advances in LiDAR scanning (Evans et al., 2016). Assertions of early tropical forest use have often been forced to rely on 'off-site' pollen, microcharcoal, and geochemical studies from lake and marine settings (Mercader, 2002a,b).

In the last two decades, excavation of some cave and rockshelter sites that have good organic preservation has permitted more direct insights into human occupation of tropical forests. Archaeobotany, archaeozoology, and technological and use-wear analysis of stone and bone tool technologies have demonstrated Late Pleistocene manipulation of toxic forest plants and long term reliance on tropical forest fauna (Barker et al., 2007; Perera et al., 2011; O'Connor et al., 2014). Similarly, stable isotope analysis of Late Pleistocene *Homo sapiens* tooth enamel has shown that they specialized in subsisting within forest ecosystems (Roberts et al., 2015). However, well-preserved cave and rockshelter sequences are absent for Early and

Middle Pleistocene sites, leaving this period something of an unknown in the context of interactions of members of our genus with tropical forest habitats.

The genus *Homo* and 'Savannahstan'

Dennell and Roebooks (2005) have argued that the first 'Out of Africa' expansion of hominins, including *Homo erectus* and the Dmanisi hominins, *c.* 1.8 Ma was driven by the development of the grasslands of 'savannahstan', stretching from East Africa and into Central Asia during the Late Pliocene and Early Pleistocene. The emergence of grasslands at this time are seen as favoring adaptations to long distance ranging and the pursuit of large mammals that are suggested to have characterized the genus *Homo* from this point onwards (Dennell and Roebroeks, 2005). Similar discussions of the colonization of Sahul by *Homo sapiens* have used foraging theory to suggest that humans rank foods by net calorific gain, always collect the highest ranked prey on encounter, and will always favor the habitat where return rates relative to search, collection and processing costs are highest (Allen and O'Connell, 2012). On this basis, tropical forest habitats have been considered marginal due to a paucity of high yield, easily processed foods (Cosgrove et al., 2007; Allen and O'Connell, 2012) (**Box 2**).

Interestingly, however, some of the earliest Early-Middle Pleistocene *Homo* fossils outside of Africa come from the tropical environments of Southeast Asia. The Sangiran Formation, characterized in the Solo Basin of eastern Java, has produced *Homo erectus* fossils dated to *c.* 1.5 Ma (Zaim et al., 2011). The Bapang and Trinil Formations have yielded further fossil evidence for *Homo erectus* in excess of 1 Ma (de Vos et al., 1994; Larick et al., 2001). Some have suggested that rainforest was the dominant vegetation type in this region between 2.6

and 1 Ma (Semah et al., 2002; Semah and Semah, 2012; Semah et al., 2016). However, there currently remains no direct evidence of tropical forest use by *Homo erectus* in this region. Where stone tools do occur, organic residue information about their use is absent (**Box 2**). Some have argued that a paucity of lithics in Southeast Asia may suggest that *Homo erectus* made use of bamboo or wooden tools, thus implying utilization of tropical forest environments (Bar-Yosef et al., 2012). Nevertheless, no such implements have yet been found and are unlikely to ever be recovered from Early to Middle Pleistocene sites in this region.

Relying on largely indirect palaeoeenvironmental records, other researchers have highlighted the prevalence of lake-edge and marsh environments that supported sedges, ferns, water-tolerant grasses and some sections of forest associated with *Homo erectus* in Southeast Asia. (Tonkunaga et al., 1985; Marwick, 2009). Aquatic and semi-aquatic vertebrates such as pygmy hippo (*Hexaprotodon*), crocodile (*Crocodylus*), the tortoise (*Geochelone*), turtles and fish (de Vos et al., 1994), and open woodland-grassland fauna including pigs (*Sus brachygnatus*), cervids (*Axis lydekkeri*), and bovids (*Bubalus palaeokerabau)* (Rozzi et al., 2013), have been associated with *Homo erectus* in this region. Finds of stone tools on the island of Flores dated to *c.* 0.8 Ma are thought to indicate a later expansion of *Homo erectus* east of Wallace's line and into more isolated tropical forest settings (Van den Bergh et al., 1996). Recent fossil discoveries at Mata Menge in Flores represent a hominin population on this island that is already representative of the divergence towards the smaller bodied *Homo floresiensis c.* 0.7 Ma, perhaps demonstrating a similar morphological adaptation to dense tropical forest environments as extant human pygmy populations (Brumm et al., 2016; van den Bergh et al., 2016). However, stable isotope analysis of faunal remains, faunal profiles, and pollen and phytolith analysis indicate that these fossils are associated with dry climates and open grassland, perhaps representing a continuation of *Homo erectus'* ecological preferences in the region (Brumm et al., 2016).

The expansion of hominins into Flores from 0.8 Ma seems best associated with declines in sea-level and forest cover rather than the development of specialized tropical forest adaptations (Marwick, 2009). During this early phase of hominin expansion, and the ongoing presence of *Homo erectus* on Sulawesi and Java *c.* 200-100 ka (Van den Bergh et al., 2016), *Homo* species appear to be part of a grassland-woodland mosaic fauna that became extinct during the shift towards modern rainforest conditions *c.* 125 ka (Westaway *et al.*, 2007; Marwick, 2009). The Punung fauna that appears from this point, includes *Pongo* (orangutan), *Hylobates* (gibbon) and *Helarctos malayanus* (sun bear) that characterize the tropical forest fauna of the region into the Holocene. It is possible that *Homo floresiensis*, now dated to 190 to 50 ka at the site of Liang Bua (Sutikna et al., 2016), was more specialized in the exploitation of these rainforest environments. Indeed, Westaway *et al.* (2009) argue that the occupation intensity of this hominin increases during increasingly wet and humid conditions, and the expansion of tropical forest (Westaway *et al.*, 2009). However, given an apparent focus on the exploitation of *Stegodon* species, prevalent across grassland and open-woodland environments across Southeast Asia, it is possible that the body size of this hominin is related purely to island insularity and a paucity of resource opportunities, rather than an association with rainforest *per se* (Larick and Ciochon, 2015).

Late Pleistocene expansion – a *global* tropical forest prehistory

It is with the emergence of *Homo sapiens* in Africa *c.* 200 ka that more evidence, in multiple regions, of tropical rainforest use and occupation by a hominin species can be found. Mercader (2002), and others (Clark, 1988; Barham 2001), have suggested that the Late

Pleistocene heavy duty Middle Stone Age Sangoan and Lupemban toolkits of Central, West, and East Africa, were used to extract tropical roots and tubers, perhaps as early as 200-250 ka. However, it has been difficult to firmly ascertain the ages of Sangoan and Lupemban toolkits that frequently come from fluvially disturbed sequences (Taylor, 2011). This is particularly problematic in the context of discerning tropical rainforest adaptations given dramatic fluctuations in the extent of the African rainforest in the past (Taylor, 2011; Taylor et al., 2016) (**Box 1**). Well-dated, regional and on-site pollen and phytolith evidence from Cameroon and Congo Kinshasa does, however, indicate a preponderance of rainforest trees, including *Canarium* sp., in association with Sangoan assemblages back to at least *c.* 28 ka (Mercader and Marti, 1999; Mercader et al., 2003).

Southeast Asia is potentially home to some of the earliest fossils of our species in tropical forest contexts, though definitive evidence is largely lacking. Confirmed early *Homo sapiens* have been found at Fuyan Cave, in Daoxian, South China, dated to *c.* 100 ka and in association with mixed tropical rainforest, woodland, and grassland fauna (Liu *et al.*, 2015), though their relationship to the dated flowstone remains disputed. A premolar possibly dating to earlier than *c.* 100 ka on the island of Java, associated with the above-mentioned Punung tropical rainforest fauna, has been argued to represent early human rainforest presence in Indonesia (Storm and De Vos, 2006; Westaway *et al.*, 2007). The recent find of *Homo sapiens* fossils at Tam Pa Ling, Laos, dated to between *c.* 60 and 46 ka, though lacking palaeoenvironmental information, represents another potentially early human fossil presence in the tropical ecologies of this region (Demeter *et al.*, 2012), as does the find of a human metatarsal within a rainforest river valley environment at Callao Cave in the Philippines (Mijares et al., 2010).

Direct evidence for the use of rainforest environments increases significantly in Southeast Asia, South Asia and Melanesia from around 45 ka. Sedimentological, palynological, botanical and faunal analysis, and use-wear studies of stone and bone toolkits at the Niah Caves, Borneo, for example, demonstrate that human foraging activities were tailored to a tropical forest environment *c.* 45 ka (Barker et al., 2007). Charred *Canarium* nutshells and starch grains from the Ivane Valley of New Guinea, and increased forest burning, also indicate the utilization of montane rainforests in Melanesia *c.* 50-40 ka (Summerhayes et al., 2010, 2016). Archaeobotanical and archaeozoological remains from the sites of Batadomba-lena and Fa Hien-lena in Sri Lanka provide evidence for a long-term reliance on tropical forest primates and tree fruits from *c.* 38-36 ka (Perera et al., 2011; Roberts et al., 2015b), while the stable isotope analysis of human tooth enamel in Sri Lanka has demonstrated that individuals not only used but also specialized in the exploitation of rainforest resources in South Asia from at least 20 ka (Roberts et al., 2015a) (**Figure 3**). Some of the earliest humans in the Americas also appear to have very quickly occupied and exploited the tropical forests of Central and South America *c.* 13 ka (Bush et al., 2011).

The expansion of *Homo sapiens* populations into a number of the world's tropical forest environments from the Late Pleistocene has also been implicated in significant modifications to the flora and fauna of these habitats. Within Southeast Asia and Sahul, tropical forest colonization is associated with fire regime change and plant community composition change in tropical forest environments (Summerhayes et al., 2010; Hunt et al., 2012). The montane tropical forests of the latter are particularly vulnerable to fires and pollen and microcharcoal evidence suggest that some of the earliest human inhabitants of the New Guinea Highlands deliberately burned tropical rainforests to promote the growth of gap-colonising plants such as *Dioscorea* spp. (yams) (Summerhayes et al., 2010). Less research has focused on Late

Pleistocene human impacts on tropical forest fauna, but it appears that humans may have contributed to the demise of tropical megafaunal populations in Southeast Asia (Louys et al., 2007) and Sri Lanka (Roberts et al., 2015b), although more work remains to be done in this area on a global and regional scale.

The time-depth of interaction between *Homo sapiens* and tropical forest ecologies has also left its mark on the biology of our species. The most significant example of this is the 'human pygmy phenotype' (Perry and Dominy, 2009). Human populations in Africa (e.g. the Efe), Southeast Asia (e.g. the Agta), South America (e.g. Yanomamo) and Australia (e.g. the Barrinneans) appear to have arrived at characteristically small final adult statures through convergent evolution due to a selective advantage conferred upon small body size in tropical forests (Perry et al., 2014; Perry and Verdu, 2016). Adaptive hypotheses stress the advantages of small body size for coping with the energetic demands these environments including: reduced caloric intake and energetic expenditure; thermal stress of a combination of heat *and* high humidity; high rates of mortality linked to disease; or locomotion through dense forest undergrowth (Perry and Dominy, 2009) (**Figure 4**). There is also growing genetic and epigenetic evidence that adaptations for small body size represent convergent evolution of phenotypes as a result of natural selection to tropical rainforest environments (Jarvis et al., 2012; Fagny et al., 2015).

Archaeological evidence from Callao Cave in the Philippines has been argued to provide evidence for the evolution of small-bodied *Homo sapiens* in a tropical forest environment *c.* 66 ka (Détroit et al., 2013). Although this fossil evidence remains contentious, early genetic divergence of rainforest hunter-gatherers from their current nearest neighbours, as well as later arguments for the role of forest fragmentation and expansion in the genetic isolation of pygmy groups in Africa (Verdu et al., 2009), demonstrate the role tropical forests can play as evolutionary 'islands' in the development of human phenotypes. While consideration of the impact of tropical forest lifeways on human phenotypes has largely been restricted to issues related to body size, thermal stress and energy balance, the additional biomechanical demands of arboreal resource extraction may drive phenotypic variation through plasticity. Modern human foragers in tropical forest environments frequently climb to tropical forest canopy levels to exploit high-value resources such as honey, fruit, and game (Venkataraman et al., 2013; Kraft et al., 2014) (**Figure 2**). This climbing has demonstrated to lead to muscular but not skeletal differences between climbers and non-climbers (Venkataraman et al., 2013), emphasizing the human capacity for habitual arboreal climbing without devolution from derived, 'obligate' bipedal skeletal adaptations.

Farmers in the forest

The relationship between *Homo sapiens* and tropical forests reached a new level of intensity during the Terminal Pleistocene and early Holocene (*c.* 12-8 ka). At this time there is increasing evidence of settlement, manipulation, and use of tropical forests by hunter-gatherer communities in Africa (Mercader, 2002a), Southeast Asia (Rabett, 2012), Melanesia (Gosden and Robertson, 1991; Summerhayes et al., 2016), Australia (Hasberle et al., 2010), and the Americas (Bush et al., 2011). Furthermore, it is during this time that mutualistic relationships between *Homo sapiens* and certain plant and animal species led to novel evolutionary pressures that culminated in the domestication of numerous species. This represents a major threshold in human evolution and in human relationships with tropical forests.

Early archaeological focus on the domestication of cereals and livestock in the Near East and Europe strongly shaped ideas about agricultural origins. In the tropics, it led to an initial focus on whether this type of agriculture could survive in the typical nutrient-poor, acidic, and wet soils of tropical forests. In South America, this debate was dominated by the suitability of *terra pretta* soils for agricultural clearance and cropping (Meggars, 1954). In Africa, studies focused on the zoonotic diseases of the Central African rainforest that may have hindered sub-Saharan expansion of pastoralism (Gifford-Gonzales, 2000; Marshall and Hildebrand, 2002). Prominent theories for the Bantu farming expansion still hinge on the tracking of waterways or grassland corridors through rainforest regions (Grollemund et al., 2014).

However, research into indigenous domestication processes within tropical forest themselves have begun to challenge and reshape thinking about the antiquity of farmer-forest relationships in the tropics (Denham et al., 2009). It is clear that crops were domesticated in the humid tropics of Melanesia (Golson, 1977), the Americas (Heckenberger & Neves 2009), and potential Australasia (Denham et al., 2003), including the banana (Musa spp.), yam (Dioscorea), taro (*Colocasia esculenta*), cassava (*Manihot esculenta*) sweet potato (*Ipomoea batatas*) and manioc (*Manihot esculenta*). In the context of extensive forest burning, clearance, and landscape modification extending back to the Late Pleistocene in regions such as New Guinea (**Box 1**), the eventual domestication of several tropical plants, notably banana and taro, should not be surprising (Denham et al., 2009).

Tropical 'agriculture' blurs the line between forager and farmer. Tropical crops were often tended by mobile societies who integrated planting with collecting and hunting; swidden (slash and burn) agriculture, which itself demands continued movement to new areas, was common. Tropical vegeculture, which focuses largely on root crops, is suggested to have attracted and supported a broad range of wild animals that were exploited as part of a 'garden hunting' pattern of subsistence that substituted for animal domestication (Linares 1976). Non- or semi-domesticated plants were often actively managed, such as palms in Amazonia (Heckenberger & Neves 2009). Direct human management of wild tropical fauna is also postulated; for example, Late and Terminal Pleistocene foragers appear to have deliberately translocated the common cuscus (*Phalanger orientalis*) to the depauparate island of New Ireland as a protein source (Heinsohn 2010). Various species of birds, fish and other aquatic species were actively managed by early Amazonians (Heckenberger & Neves 2009).

The intensive exploitation of tropical forest plant and animal resources expanded into emerging global networks that appeared in the two millennia AD. Tropical forest commodities from the islands of Southeast Asia became some of the most highly valued commodities of Old World trade by the first millennium AD. The so-called 'spice' or 'clove' routes saw cloves from the Philippines, cinnamon from South China, and cassia and aloeswood from Java spread from the tropical forests of Southeast Asia across the Indian Ocean to the Middle East, Europe, and the East coast of Africa (Hoogervorst, 2013). Bananas also appear to have moved from Southeast Asia into Africa at this time (Fuller et al., 2010). Likewise, the Maya may have expanded into lowland tropical forest specifically to exploit rainforest commodities, including a broad range of medicines, perfumes, dyes, and other exotic items (Voorhies, 1982). These trade networks, and their impacts on forests, became increasingly commercialized with the maritime expansion of colonial powers, often having devastating impacts on forests and local people such as in the case of South American rubber exploitation (Hemming, 2009).

Conclusion: Human forests – a path to destruction?

Tropical forests apparently represent the cradle for all of the great apes, including the hominin clade, in Africa. Although it has been suggested that some of the earliest members of the genus *Homo* to move beyond Africa made use of tropical forests in Southeast Asia, direct evidence for this is thus far lacking. While stable isotope analysis of *Homo erectus* and *Homo floresiensis* fossils, and long-term, multi-proxy palaeoenvironmental sequences in direct association with these hominins and their technologies, may provide further insight into the forest adaptations of these species in future, there remains something of a gap in our knowledge of the interaction of our genus with these environments until the evolution of our species in the Late Pleistocene. If this gap is real, rather than any significant shifts in cognition (Klein, 2000), this may further highlight the unique adaptive flexibility of *Homo sapiens* that is perhaps related to its ability to form complex social networks (Rabett, 2012). During the Late Pleistocene *Homo sapiens* not only appears to have traversed extreme environments, including deserts (Groucutt et al., 2015), tundra (Fu et al., 2014), and tropical forests, but specialized in the long-term exploitation and manipulation of these habitats.

This simultaneous plasticity and focus is also seen in the unique capacity of our species to construct and shape its own ecological niches, changing environments, flora and fauna (Boivin et al., 2016). In tropical forest environments, however, this niche construction can have disastrous consequences. Today, these environments continue to support global human demand for ecosystem services, including ‘supporting’ services such as soil formation and nutrient and water cycling, ‘provision’ services in the form of food, fuel, genetic diversity, and freshwater, and ‘cultural’ services of aesthetic value (Gardner et al., 2009). Tropical forests are now mined, both literally and metaphorically, for precious metals, gemstones, and oil, while forest clearing takes place on industrial scales to grow cash crops responding to global demands for hardwood, medicines, coffee, and chocolate (Hemming, 2009). The increasing commercialization of tropical forests by human societies today threatens these environments through mechanical deforestation, chemical pollution, and the influence of tree crop monoculture on plant genetic diversity and disease resistance (Ghazoul and Shiel, 2010). The expansion of palm oil plantations in Southeast Asia is a high profile example of how rapidly vast areas ancient tropical forest diversity can be obliterated through clearance, monoculture, and unintentional fires.

Humans have also increasingly placed themselves, and their ever-growing population numbers and urban settlements, within tropical forests. From the Late Holocene, a range of societies in the prehistoric Amazon developed features such as integrated regional social systems, monumentality, elites, and extensive networks of exchange (Heckenberger and Neves, 2009). The lowland Maya also inhabited dense tropical forest, and forest declined significantly with rising population numbers (Dunning et al., 2012). Numerous other examples of low-density agrarian cities dominated the tropical forests of lowland Mesoamerica, Sri Lanka and mainland Southeast Asia between the late first millennium BC and the mid-second millennium AD (Fletcher, 2012). While these urban experiments proved relatively resilient, the sustainability of ever-expanding urbanism in the tropics of the modern world may be compromised by ongoing forest clearance for building materials, farmland and urban space. The fight to preserve these environments is center stage in the test as to whether the unique global ecological impact of our species will be sustainable in the face of climatic, environmental, and demographic threats, in part, of its own making.

Acknowledgments

For financial support, we acknowledge the Natural Environmental Research Council (no. 1322282 to PR), the Boise Fund (to PR), the European Research Council (no. 206148 to NB, no. 617627 to JS, no. 295719 to MP), and the Leakey Foundation (to JLT). We are grateful to

John Pouncett and Elisabeth Thompson for their help with Figures 1 and 2, as well as Matt Sponheimer for comment on Figure 3.

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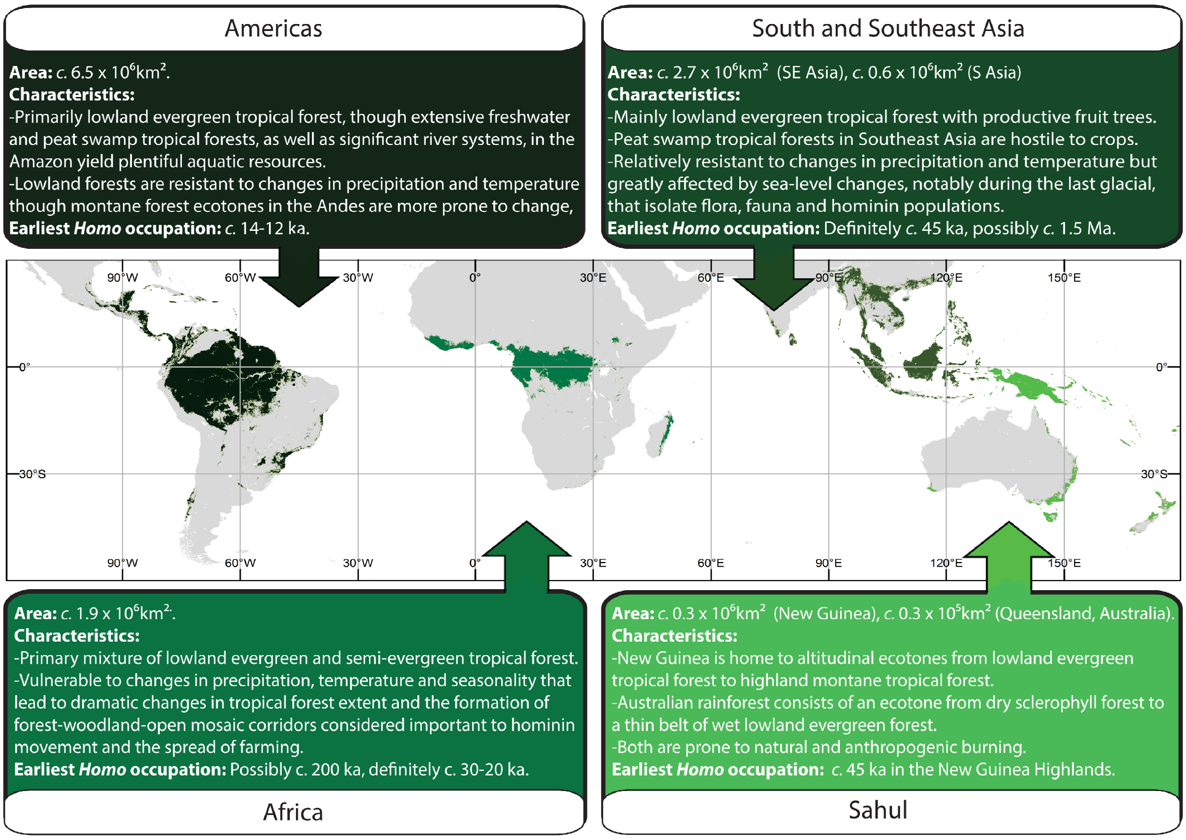
List of Figures:

Figure 1. Current distribution of tropical forest determined by the MODIS (Moderate Resolution Imaging Spectroradiometer) Land Cover MCD12Q1 majority land cover type 1, class 2 for 2012 (spatial resolution of 500 m). Downloaded from the US Geological Survey Earth Resources Observation System (EROS) Data Center (EDC). Estimations of areas for each region is adapted from Mayaux et al.'s discussion of the TREE II Project data for humid tropical forest extent in the Americas, Africa, and Southeast Asia in 1997 (Mayaux et al., 2005), Foody and Curran's (1994) data for the extent of tropical forest in South Asia in 1990,[95] Shearman et al.'s data for the extent of 'rain forest' in New Guinea in 2002 (Shearman et al., 2009), and the WWF's estimation of tropical forest extent in Northeastern Australia (http://www.worldwildlife.org/ecoregions/aa0117).



Americas

Area: *c.* 6.5 x 10^6km^2.
Characteristics:
-Primarily lowland evergreen tropical forest, though extensive freshwater and peat swamp tropical forests, as well as significant river systems, in the Amazon yield plentiful aquatic resources.
-Lowland forests are resistant to changes in precipitation and temperature though montane forest ecotones in the Andes are more prone to change,
Earliest *Homo* occupation: *c.* 14-12 ka.

South and Southeast Asia

Area: *c.* 2.7 x 10^6km^2 (SE Asia), *c.* 0.6 x 10^6km^2 (S Asia)
Characteristics:
-Mainly lowland evergreen tropical forest with productive fruit trees.
-Peat swamp tropical forests in Southeast Asia are hostile to crops.
-Relatively resistant to changes in precipitation and temperature but greatly affected by sea-level changes, notably during the last glacial, that isolate flora, fauna and hominin populations.
Earliest *Homo* occupation: Definitely *c.* 45 ka, possibly *c.* 1.5 Ma.

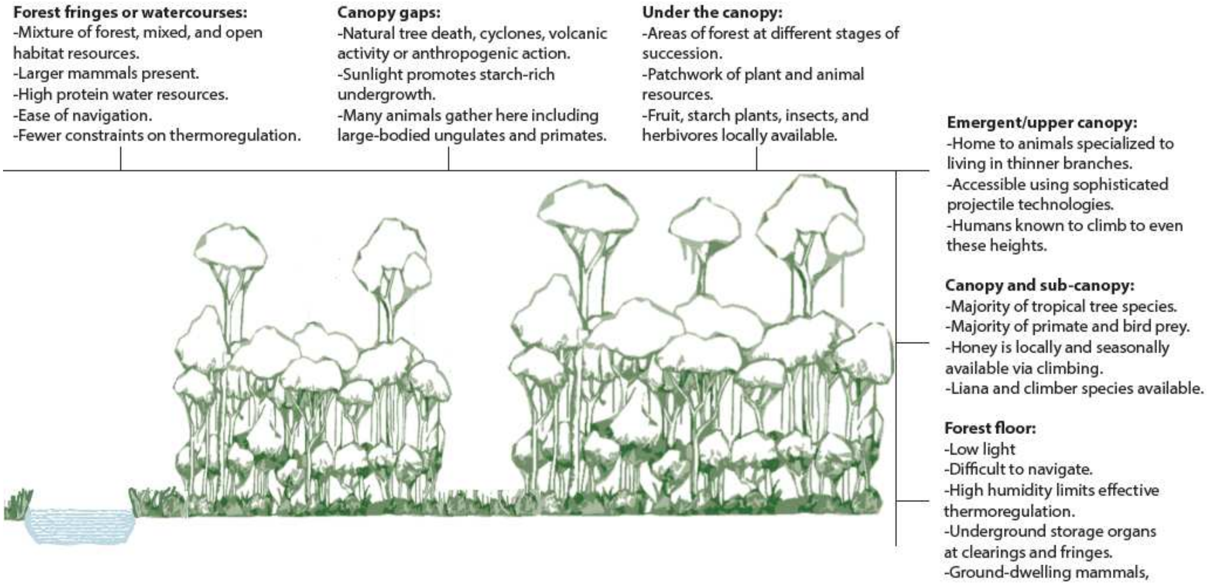
Area: *c.* 1.9 x 10^6km^2.
Characteristics:
-Primary mixture of lowland evergreen and semi-evergreen tropical forest.
-Vulnerable to changes in precipitation, temperature and seasonality that lead to dramatic changes in tropical forest extent and the formation of forest-woodland-open mosaic corridors considered important to hominin movement and the spread of farming.
Earliest *Homo* occupation: Possibly c. 200 ka, definitely c. 30-20 ka.

Africa

Area: *c.* 0.3 x 10^6km^2 (New Guinea), *c.* 0.3 x 10^5km^2 (Queensland, Australia).
Characteristics:
-New Guinea is home to altitudinal ecotones from lowland evergreen tropical forest to highland montane tropical forest.
-Australian rainforest consists of an ecotone from dry sclerophyll forest to a thin belt of wet lowland evergreen forest.
-Both are prone to natural and anthropogenic burning.
Earliest *Homo* occupation: *c.* 45 ka in the New Guinea Highlands.

Sahul

Figure 2. The distribution of plant and animal resources, and conditions, relevant to human subsistence in a tropical forest ecology.



Forest fringes or watercourses:
-Mixture of forest, mixed, and open habitat resources.
-Larger mammals present.
-High protein water resources.
-Ease of navigation.
-Fewer constraints on thermoregulation.

Canopy gaps:
-Natural tree death, cyclones, volcanic activity or anthropogenic action.
-Sunlight promotes starch-rich undergrowth.
-Many animals gather here including large-bodied ungulates and primates.

Under the canopy:
-Areas of forest at different stages of succession.
-Patchwork of plant and animal resources.
-Fruit, starch plants, insects, and herbivores locally available.

Emergent/upper canopy:
-Home to animals specialized to living in thinner branches.
-Accessible using sophisticated projectile technologies.
-Humans known to climb to even these heights.

Canopy and sub-canopy:
-Majority of tropical tree species.
-Majority of primate and bird prey.
-Honey is locally and seasonally available via climbing.
-Liana and climber species available.

Forest floor:
-Low light
-Difficult to navigate.
-High humidity limits effective thermoregulation.
-Underground storage organs at clearings and fringes.
-Ground-dwelling mammals,

Figure 3. Inferred stable carbon isotope data of vegetation for a) modern chimpanzees and gorillas in western-central Africa (Macho and Lee-Thorp, 2014; Oelze et al., 2014), extinct apes (*Sivapithecus* (Nelson, 2007) *Gigantopithecus* (Nelson, 2014; Bocherens et al., 2015) b) African hominin species (from data compiled in Sponheimer *et al.* 2013) and c) *Homo sapiens* in Late Pleistocene/Holocene Sri Lanka (data from Roberts *et al.*, 2015a) and Holocene Southeast Asia (Krigbaum, 2001). A correction of -13‰ (shown by Cerling and Harris (1999) for non-ruminant ungulates) has been applied to the fossil enamel data, while a correction of -4.5‰ has been applied to modern ape hair data. This latter value includes a correction of -3‰ for diet-hair enrichment (as in Sponheimer *et al.* 2003) and a further -1.5‰ in order to correct for the fossil fuel effect where appropriate (Francey et al., 1999).

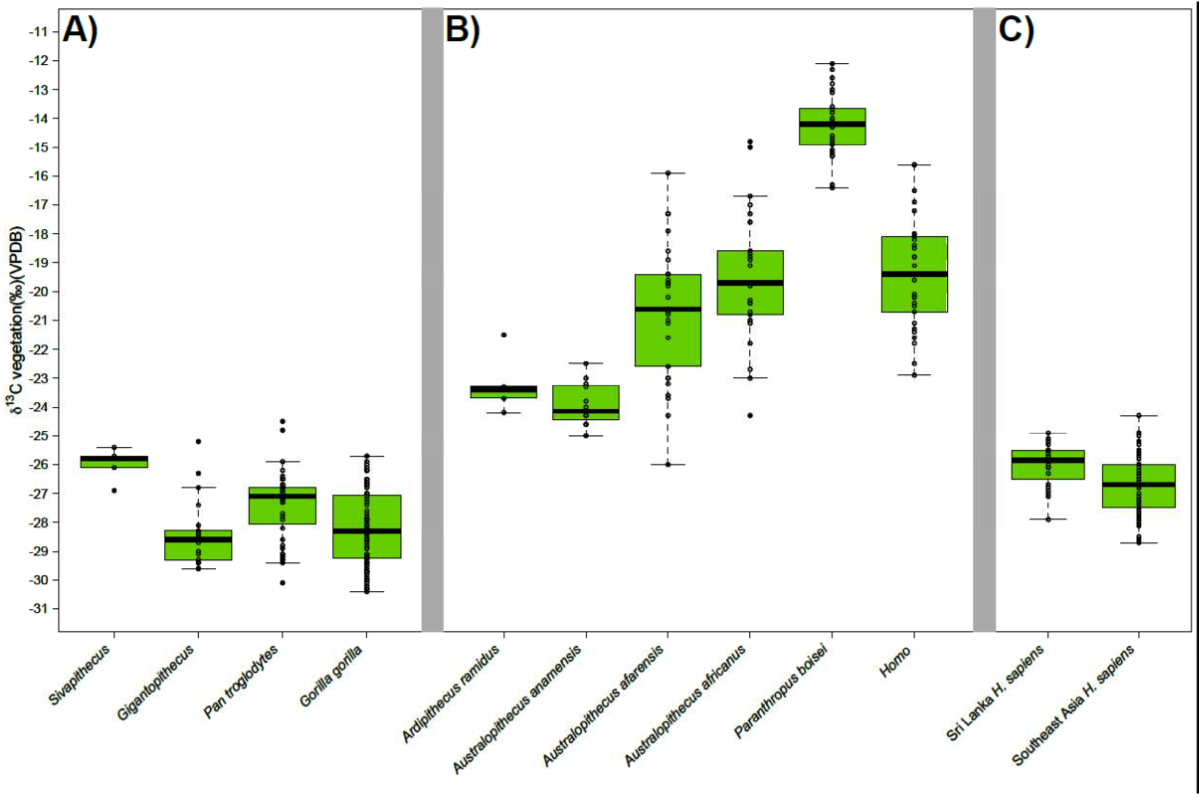


Figure 4. Selective pressures hypothesized to favor small body size in tropical forests. In tropical forest environments: 1) food scarcity may lead to selective pressure on body size for reduced energy requirements and reduced caloric intake; and the energetic demands of forest mobility relative to dietary intake may lead to further selective pressure and reduced energy expenditure; 2) high daily maximum temperature combined with high humidity makes evaporative cooling from sweating ineffective, which may favor small body size to decrease metabolic heat generation; or 3) high mortality and low life expectancy may favor life history strategies of earlier reproduction and growth cessation.