Macaques at the margins: the biogeography and extinction of *Macaca sylvanus* in Europe.

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ABSTRACT

The genus *Macaca* (Primates: Cercopithecidae) originated in Africa, dispersed into Europe in the Late Miocene and resided there until the Late Pleistocene. In this contribution, we provide an overview of the evolutionary history of *Macaca* in Europe, putting it into context with the wider late Miocene, Pliocene and Pleistocene European monkey fossil record (also comprising *Mesopithecus*, *Paradolichopithecus*, *Dolichopithecus* and *Theropithecus*). The Pliocene and Pleistocene European *Macaca* fossil material is largely regarded as *Macaca sylvanus*, the same species as the extant Barbary macaque in North Africa. The *M. sylvanus* specimens found at West Runton in Norfolk (53°N) during the Middle Pleistocene are among the most northerly euprimates ever discovered. Our simple time-budget model indicates that short winter day lengths would have imposed a significant constraint on activity at such relatively high latitudes, so macaque populations in Britain may have been at the limit of their ecological tolerance. Two basic models using climatic and topographic data for the Last Interglacial and the Last Glacial Maximum alongside Middle and Late Pleistocene fossil distributions indicate that much of Europe may have been suitable habitat for macaques. The models also indicate that areas of southern Europe in the present day have a climate that could support macaque populations. However, *M. sylvanus* became locally extinct in the Late Pleistocene, possibly at a similar time as the straight-tusked elephant, *Palaeoloxodon antiquus*, and narrow-nosed rhinoceros, *Stephanorhinus hemitoechus*. Its extinction may be related to vegetation change or increased predation from *Homo*, although other factors (such as stochastic factors occurring as a result of small population sizes) cannot be ruled out. Notwithstanding the cause of extinction, the European macaque may thus be a previously overlooked member of the Late Pleistocene faunal turnover.

1.1. Introduction

The Pleistocene witnessed significant biogeographic shifts in primate fauna, not least the extinction of all non-human primates in Europe. The rapid climatic fluctuations and corresponding changes to landscapes, environments and physical features (such as land bridges) during the Pleistocene clearly had the potential to shape European primate biogeography. It is also highly likely that concomitant changes to ecological communities, leading to alterations in competition and predation (Meloro and Elton, 2012), also influenced primate distributions. Alan Turner, although best known as a specialist in carnivorans, had an encyclopaedic knowledge about and interest in the fauna of the Neogene and Quaternary Old World. This included primates, as members of the diverse and dynamic ecological communities of the European Pleistocene. Thus, in this review, in honour and fond memory of him, we provide an overview of monkey evolutionary history and biogeography in the European Late Miocene, Pliocene and Pleistocene, with a specific focus on the distribution and extinction of the Barbary macaque (*Macaca sylvanus*).

1.2. A brief introduction to the Cercopithecidae and the genus *Macaca* in Europe

Macaca is a genus within the Old World monkey family Cercopithecidae (cercopithecids). The cercopithecids arose in the Miocene, and molecular data indicate that the two subfamilies (Colobinae and Cercopithecinae, the colobines and cercopithecines respectively) split around 16 Ma (Raaum et al., 2005). The cercopithecines, the subfamily to which *Macaca* belongs, are further subdivided into two tribes, the Papionini (comprising modern macaques, baboons, mangabeys, gelada, drills and mandrills as well as an extensive extinct radiation) and the Cercopithecini (guenons). Fossil evidence for the early events in cercopithecine evolution is sparse, but molecular data suggest that the split between papionins and guenons occurred between around 10 and 13 Ma (Tosi et al., 2005; Raaum et al. 2005). Until the late Miocene, the Old World cercopithecid fossil record is concentrated entirely in Africa, so it is assumed that the family evolved there. The genus *Macaca* originated in the late Miocene, probably in North Africa, diverging from other papionins around 7.6 ± 1.3 Ma (Tosi et al., 2005), with the earliest macaque fossils found at the late Miocene sites of Menacer (Algeria, ?*Macaca* sp.) and Wadi Natrum (Egypt, *Macaca lybica*) (Delson, 1974; Fooden, 2007).

Other non-human catarrhine primates, the hominoids (apes) and the pliopithecoids (relatively large primates that radiated in the Eurasian Miocene but have no living descendants), were present in Europe for a significant part of the Miocene (Begun, 2002; Casanovas-Vilar et al., 2011). However, the fossil record suggests that monkeys only dispersed into Europe in the late Miocene. The colobine genus *Mesopithecus* is the first monkey evident in Europe, at around 8.5 Ma (Delson et al., 2000). Given that Asian and

African colobines diverged in Africa around 11 Ma (with a confidence limit of between 9.6 and 12.3 Ma; Raaum et al., 2005), the ancestor of *Mesopithecus* probably dispersed into Eurasia reasonably soon after this split, speciating in Europe. Often described as 'macaque-like', *Mesopithecus* was likely to have used arboreal substrates but was also terrestrially adept (Youlatos et al. 2012; Alba et al. 2014). Although the ancestral locomotor condition of *Mesopithecus* is still far from clear, it is likely that its locomotor flexibility contributed significantly to its ability to disperse into Eurasia and exploit the varied environments it found there (Youlatos et al. 2012), reinforced by the relatively catholic nature of its diet (Merceron et al., 2009). It appears to have been tenacious, present in much of Europe for several million years during the late Miocene and Pliocene, and reaching as far north as Red Crag in Norfolk, Britain (Delson, 1994). Although *Mesopithecus* has been linked phylogenetically with African colobines (Strasser and Delson, 1987), it is probably more closely related to the snub-nosed monkeys (*Rhinopithecus* sp.) of south east Asia (Jablonski, 1998). Given this, it appears that the descendants of *Mesopithecus* shifted their range east, into Asia, at some point in the Pliocene or Pleistocene.

Macaca first appeared in Europe during the latest Miocene (Delson, 1974; Köhler et al. 2000; Alba et al. 2014), after the dispersal of *Mesopithecus*, and survived there until the late Pleistocene (Fooden, 2007). The apes and pliopithecoids became extinct in Europe in the mid Late Miocene, with the last known specimens dated to around 7 million years ago (Begun, 2002; Casanovas-Vilar et al, 2011), around one million years before macaques dispersed into Europe. Even considering the presence of *Mesopithecus* in Europe earlier than this, it is unlikely that monkeys dispersing into Europe during the Late Miocene directly replaced apes and pliopithecoids and caused their extinctions. Instead, it is possible that late

Miocene environments in Europe became more homogeneous, therefore reducing ape diversity (Merceron et al., 2010) and providing concomitant opportunities for monkeys to radiate. Indeed, the biology and behaviour of cercopithecids, including their more rapid life history schedules (Jablonski et al., 2000) and their lack of dependence on ripe fruit (Andrews, 1981), appear especially well-suited to exploiting the changing and increasingly seasonal environments that characterised Europe in the latest Miocene (Marigó et al. in press).

In addition to *Mesopithecus* and *Macaca*, three other monkey genera were present in Europe during the Pliocene and into the Pleistocene (Delson, 1974; Gibert et al., 1995; Jablonski, 2002; Eronen and Rook, 2004; Figure 1): the colobine *Dolichopithecus*, and the cercopithecines *Paradolichopithecus* and *Theropithecus*. *Dolichopithecus*, larger than *Mesopithecus* and also terrestrial, is found at Pliocene sites in western and central Europe, Macedonia and Greece (Jablonski, 2002). Fossils of *Paradolichopithecus*, larger than *M. sylvanus* and highly terrestrial, yet sharing many craniodental features with macaques, have been recovered from a wide area of Eurasia, including France, Greece, Romania and Tajikistan (Jablonski, 2002). *Paradolichopithecus* may be synonymous with another fossil cercopithecine, *Procynocephalus*, and if so had an extremely wide distribution across Eurasia, reaching as far as China (Jablonski, 2002). The large-bodied, predominantly grass eating and terrestrial genus *Theropithecus* had an extensive radiation in the Pliocene and Pleistocene of Africa and is also known with reasonable certainty from India (Gupta and Sahni, 1981; Delson, 1993) and Cueva Victoria in Spain (Gibert et al., 1995). However, it is controversial whether *Theropithecus* ever had a wider presence in Europe: it is identified from only one other site, Pirro Nord in Italy (Rook et al., 2004), represented by three vertebrae, and it cannot be ruled out that these specimens are actually another species, possibly *Paradolichopithecus* (Patel et al., 2007). A calcaneum from a large cercopithecine has also been reported from 'Ubeidiya in Israel; while referred to cf. *Theropithecus* sp. the possibility that it represents *Paradolichopithecu*s cannot currently be excluded (Belmaker, 2010).

It is likely that members of the genus *Macaca* initially dispersed from Africa into Europe and Asia across or around the Mediterranean region (Delson, 1974). The Miocene record of cf. *Macaca* in Europe is sparse, with only two instances recorded (Alba et al., 2014). All the Pliocene and Pleistocene European macaques are considered to belong to the *Macaca sylvanus* species group (Szalay and Delson, 1979; Rook et al., 2001; Jablonski, 2002), with specimens assigned to various subspecies, including *M. s. pliocena* (Marigó et al. in press), *M. s. sylvanus* and *M. s. florentina* (Alba et al. 2011). The exception is the endemic insular Sardinian form with an unusually small cranium, *Macaca majori,* which is still part of the *M. sylvanus* group but usually elevated to species rank (Rook and O'Higgins, 2005). As we are interested in the presence of the genus *Macaca* in the Pleistocene rather than focusing on a particular species or subspecies, findspots of *M. majori* are included with those of *M. sylvanus* throughout our study. *M. sylvanus*, the Barbary macaque, exists to the present day in North Africa but has a highly restricted distribution, confined to small areas in Morocco and Algeria (Fooden, 2007), although there is an introduced population on Gibraltar (Modolo et al., 2005). Modern *M. sylvanus* is unusual in being the only African macaque: the modern stronghold of the genus is in south and south east Asia, where it is represented by over 20 species (Brandon Jones et al., 2004; IUCN 2013; Table 1), and no macaques (or indeed non-human primates) survive in natural populations in Europe today.

In the late Miocene *Mesopithecus* may have been a significant competitor to *Macaca* in Europe. Few sites have both species (Eronen and Rook, 2004; Delson et al., 2005; Alba et al., 2014), perhaps indicating that *Mesopithecus* may have initially competitively excluded *Macaca*. Early Pliocene *Macaca* co-occurs with *Dolichopithecus* and *Mesopithecus* at Montpellier, and in Middle-Late Pliocene deposits with *Mesopithecus* at Triversa Fornace RDB in Italy and with *Dolichopithecus* at Balaruc-2, France (Eronen and Rook, 2004; Delson et al., 2005). *Macaca* and *Paradolichopithecus* are associated in the Early Pleistocene deposits at Senèze (Delson et al., 2005), and possibly at Late Pliocene Cova Bonica, Spain, although further work must be done to ascertain the presence of *Macaca* there (Marigó et al. in press). It is possible that *Mesopithecus*, *Paradolichopithecus*, *Dolichopithecus* and *Macaca* have all been recovered from Canal Negra I, Spain (Guillén Castejón, 2010), although the karstic nature of this locality indicates time-averaging, and the taxonomic attributions of specimens from the site are not yet secure (Marigó et al. in press). Although *Mesopithecus*, *Dolichopithecus* and *Paradolichopithecus* were potential competitors with *Macaca*, differences in body size and attendant variations in diet and habitat use may have offset direct competition, as is evident in many modern primate communities (Reed, 1999).

1.3. *Macaca* distribution in Europe

The Messinian salinity crisis, between around 5.9 and 5.3 Ma, in which the level of the Mediterranean Sea fluctuated and occasionally dried out, may have facilitated macaque dispersal from North Africa. However, very few macaque specimens have been recovered from late Miocene deposits in Europe, with the only two fully published finds being from Almenara-Casablanca M in Spain (Köhler et al., 2000) and Moncucco Torinese in Italy (Alba et al., 2014). *Macaca* has also been reported from the late Miocene locality of Puerto de la Cadena, Spain (Mancheño et al. 2013). By the early Pliocene *M. sylvanus* had a circum-Mediterranean distribution (*sensu* Delson, 1974), including the modern Black Sea region and southern France (Figure 2).

By the earliest Pleistocene (2.5Ma (following Gibbard et al. (2010)), to 1.5 Ma), *M. sylvanus* was present around the Mediterranean, in peninsular Italy, Sardinia and Spain, and also as far north as Tegelen in the Netherlands (Schreuder, 1946; van den Hoek Ostende and de Vos, 2006; Figure 2). Towards the middle and end of the Early Pleistocene *M. sylvanus* maintained its wide distribution, occupying the whole of what is now mainland Europe (Figure 2). This continued into the Middle Pleistocene (Figure 3), with macaque fossils also being found in south-eastern and eastern Britain. By the end of the Middle and start of the Late Pleistocene (0.2 – 0.1 Ma), the secure macaque fossil sites are restricted to North Africa and Spain (Figure 3), which could represent refugia but also could be a sampling or taphonomic artefact, as macaque fossils from the Late Pleistocene (0.13-0.01) have been recovered from a wider range of European sites, albeit with a less northerly distribution than is evident in the Middle Pleistocene (Figure 3). The European primate fauna becomes much less diverse in the Pleistocene, with *Macaca* being the only primate remaining probably by the Middle and definitely by the Late Pleistocene (Figure 1). Of the other two primate genera present in the European Pleistocene, *Paradolichopithecus* becomes extinct in the Early Pleistocene (Jablonski, 2002). *Theropithecus* may also be gone from the European fossil record by the end of the Early Pleistocene, although the dating of the only secure site, Cueva Victoria in Spain is somewhat controversial (see Hughes et al., 2008 for a summary).

M. sylvanus seems the most tenacious of all the European cercopithecine monkeys, surviving for longest in the fossil record and having the widest overall geographic distribution. However, presence and absence data only provide a partial picture of 'success'. The fossil record of *Macaca* is relatively sparse, and its overall abundance in Europe is far from clear. Isolated teeth unsurprisingly form the bulk of known specimens in Europe and there are relatively few postcranial elements. At no site in Europe do macaque fossils appear common. This is similar to the fossil records of other European monkeys in the Pliocene and Pleistocene but is in contrast to the relative abundance of *Mesopithecus* in at least parts of Europe during the Miocene (Koufos, 2009), and the large amount of material attributed to some monkey species in Africa, such as *Theropithecus oswaldi* (Delson, 1993). It is possible – but by no means demonstrated – that the sparse fossil record of monkeys in the European Pliocene and especially Pleistocene reflects their rarity in life (Meloro and Elton, 2012). Primates are a tropical radiation, so the relatively poor representation of later European primates compared to those in the tropics (or even within Europe in the warmer Miocene) may have been due, at least in part, to the 'marginal' nature of primate occupation in temperate regions.

To explore extinct European macaque distributions in more detail, we reconstructed species ranges for fossil *M. sylvanus* on the basis of recorded fossil finds. Each site was assigned to a time period (see Supplementary Information for full site list, geographic coordinates and time period). Simple polygons based on findspots at the geographic extremes of the range were constructed in QGIS Application (QGIS Development Team, 2013) using the World Equidistant Cylindrical (Sphere) projection. North African sites were not included in the polygons to avoid over-estimating ranges by including the Mediterranean Sea itself, although British sites were included, as it formed a peninsula on the edge of mainland Europe during much of the Pleistocene (Funnell, 1995; Pettitt and White, 2012). The area of each polygon was calculated using the geometry 'area' function in QGIS. Since the modern *M. sylvanus* range is so small, the species range of all other modern macaque species (including *M. mulatta* and *M. fuscata* that both have ranges that extend into temperate latitudes), were calculated to provide context. This was done in ArcGIS 9.1 from distribution polygons based on approximate species range data downloaded from the IUCN Red List (IUCN, 2013).

The fossil site distribution / modern species range areas are given in Table 1. It is of course possible that pooling the fossil sites into time periods has resulted in over-estimates of actual geographic range for a given point in time, but even with this possible bias towards larger range sizes, at no time during the Pleistocene did the *M. sylvanus* distribution approach the size of the modern *M. mulatta* geographic range. However, the calculated ranges based on fossil sites for each time period are commensurate with the species ranges of other modern macaque species frequently considered to be widespread (e.g. *M. fascicularis*; Ong and Richardson, 2008), and are also towards the upper end of modern African primate species range areas (Elton and Dunn, in press).

Examining macaque distribution in Europe during the Pleistocene opens up some fascinating questions. Given that Late Pleistocene sites are spread over an area of over 1,000,000 km^2, well in excess of several modern macaque geographic ranges, our first question is why they became extinct in Europe. Our second question is why fossil macaque findspots are not present above around 53°N in Europe. In this article, we aim to shed some light on these questions, although attempting a full analysis of the factors that could have potentially contributed to *M. sylvanus* distribution in the Pleistocene is challenging, given the number of influential variables. Based on socioecological observations of modern monkeys, these include vegetation distribution and quality (providing suitable food and habitat), day length, competitors, predators, climate (primarily temperature and precipitation) and elevation. However, future work, some of which we are undertaking already (isotopic studies of fossil macaque diets: Chenery et al., 2008), will focus on reconstructing the palaeobiology of European macaques directly rather than relying solely, as we do here, on models and analogy with extant conspecifics and congeners.

2. Surviving on the margins: diet, habitat and vegetation

Modern macaques, for the most part, are primary consumers - they depend on plant matter for food, even though they may supplement their diets with faunal resources such as insects, fish and eggs (see for example Fooden, 2000; O'Regan et al., 2008), and recently *M. sylvanus* has been observed hunting and eating rabbits and chicks (Young et al. 2012). Most primates are ecologically dependent on trees, with modern macaques proving no exception to this. We therefore assume that the same broad principles were true for the now extinct populations of *M. sylvanus* in Europe. While some Old World monkeys that radiated in the Pliocene and Pleistocene, such as *Theropithecus,* have been extensively studied, there has been much less direct research on the palaeobiology of macaques. In this review, therefore, we depend on analogy with living members of the genus *Macaca* to draw broad conclusions about the biology and behaviour of fossil macaques that may help to shed light on their biogeography. However, it must not be uncritically assumed that the behaviours of modern animals, even within the same species, are equivalent to those of extinct forms. Indeed, alongside the possibility that significant behavioural evolution has occurred during the tenure of the species, living populations of *M. sylvanus* are well known to be living in highly anthropogenically modified habitats that pose a significant threat to long-term survival (Butynski et al., 2008). Thus, they may not be ideal models for ‘typical’ behaviour within the species, and to mitigate this we make inferences based on examples drawn from several modern primate species as well as palaeobiological data from other extinct primates and mammals.

The modern ability of macaques to survive in environments that can be viewed as suboptimal or marginal for a largely tropical radiation is due in part to their highly catholic feeding behaviour (Jablonski, 2002; O’Regan et al., 2008). Members of the genus consume a wide range of foods including ripe fruit, flowers, mature and immature leaves, seeds and bark, invertebrates and occasionally vertebrates (Hill, 1997; Hanya et al., 2003). There are often marked changes in macaque diet determined by habitat: modern macaques found in tropical regions apparently consume more fruit than do macaques in temperate or more marginal zones, which tend to be more folivorous (Hill, 2003), and stable isotope studies of hair from museum specimens of *M. mulatta* indicate that individuals living at higher latitudes are more likely to supplement their diets with C4 (tropical grass-based) food resources (O’Regan et al., 2008). In temperate latitudes, plant productivity is lower than in the tropics, and available foodstuffs may fluctuate considerably across the year (Ulijaszek et al., 2012). At times of low productivity, including the winter, macaques may turn to non-preferred food with a lower nutritional value. Both *M. fuscata* and modern *M. sylvanus* appear to prefer fruits and/or seeds such as acorns when available but have diets dominated by leaves (Hanya et al., 2011). As this appears to be a common dietary pattern in temperate primates (Hanya et al., 2011), we can assume that European macaques in the Plio-Pleistocene had similar dietary composition, preferentially incorporating high energy fruits and/or seeds in the diet when available but with more ubiquitous leaves as an important staple. Some modern temperate primates, notably *M. sylvanus* and the snub-nosed monkey *R. roxellana*, also incorporate significant quantities of lichens into their diets, as a year-round fallback food and a dominant dietary component in winter (Grueter et al., 2009). Not all modern 'feeding' behaviours may have been present in past populations, however. For example, the bark stripping and consumption of cambium and sap observed in modern Barbary macaques is much more likely to be a response to exclusion from water sources because of human encroachment than because bark is an important fallback food (Camperio Ciani et al., 2001).

Modern *M. sylvanus* inhabits deciduous (cedar-oak, oak) and coniferous (fir) forests in North Africa (Menard, 2002), and *M. fuscata* also uses both types of forest (Hanya, 2004). Although primates are associated primarily with angiosperm exploitation (Ulijaszek et al., 2012), gymnosperm products including fir foliage, fir seeds and yew fruits are significant dietary components for some extant *M. sylvanus* populations in Morocco (Mehlman, 1988) and coniferous forest is important habitat not only for some modern temperate macaque groups but also some species of temperate-living colobines in the genus *Rhinopithecus* (snub-nosed monkeys) (Kirkpatrick, 1995). This suggests that Pleistocene *M. sylvanus* could have inhabited both deciduous and coniferous forest. At Middle Pleistocene Hoxne (MIS 11), pollen records indicate a switch from deciduous woodland, to alder carr (small scrub / shrub) forest, then cold climate Arctic / Alpine flora including dwarf birch and dwarf willow

(Ashton et al., 2008). The faunal assemblage containing *M. sylvanus* is indicative of a mixed deciduous woodland or open grassland region (Ashton et al., 2008). Fir pollen has also been recovered from Hoxne although its stratigraphic position is not clear (Ashton et al., 2008). At Tegelen, an Early Pleistocene northern European *Macaca* site, in situ plant remains have been assigned to pine, spruce, fir, cypress, magnolia, elm, hackberry, maple, and other deciduous woodland species (van der Burgh, 1974). While the fauna from Tegelen is probably time-averaged (van den Hoek Ostende and de Vos, 2006), if present, such plant species would have provided good habitat and sources of food for *Macaca sylvanus*.

The plant species at any given location obviously fluctuated according to glacial cyclicity in the Pleistocene. This is evident, for example, in well-studied Middle Pleistocene deposits of the Upper Rhine Valley where pollen spectra indicate late-glacial flora such as juniper and birch giving way to an interglacial sequence that includes oak and elm, with pine, spruce, beech and other genera now known only from south east Asia sampled elsewhere in the sequence (Knipping, 2008). The plasticity evident in modern *M. sylvanus* (Menard, 2002) indicates that past conspecifics would have been ideally placed to ‘ride out’ at least the initial vegetation changes that occurred during the transition from interglacial to glacial conditions before dying out or retreating to refugia, and may have been able to move back into previous occupation areas quite rapidly with glacial retreat. Even in environments dominated by Arctic / Alpine flora, Pleistocene macaques, as highly eclectic feeders, may have had access to many edible foodstuffs, including dwarf shrub leaves, bilberries and snowberries, flowers, herbs, lichens and fungi.

3. Considering distributions and colonising Britain: time budgeting, group sizes and the influence of day length

Extant macaques are found at latitudes higher than any other modern non-human primate, with the Japanese macaque (*M. fuscata,* also known as the snow monkey) reaching as far as 41˚N. Fossil primates have been found at even higher latitudes, including an extensive assemblage of early Miocene platyrrhine fossils recovered from the Santa Cruz Formation in Patagonia 51°S (Fleagle and Tejedor, 2002; Kay et al., 2012). In the Eocene, when global climate was much warmer and a tropical forest belt is likely to have existed on the high latitude landbridge from Europe via Greenland to America, euprimates (primates of modern aspect) were distributed above the Arctic Circle (Smith et al. 2006). Nonetheless, Middle Pleistocene *Macaca* and Pliocene *Mesopithecus*, found in Britain (Norfolk) at a latitude of around 53°N, are still among the most northerly euprimates ever discovered, and may have pushed to extremes the geographic limit of post-Eocene non-hominin primate colonisation.

Macaques are found in Britain only during the Middle Pleistocene. Two specimens have been recovered from West Runton in Norfolk, one from the Early Middle Pleistocene (MIS 17 or 15) Freshwater-Bed and the other from the overlying gravel (Stuart, 1996; Stuart and Lister, 2010). *Macaca* appears absent from MIS 13 (Boxgrove) but is found in MIS 11 at both Hoxne and Swanscombe (Ardito and Mottura, 1987) and in MIS 9 at Cudmore Grove, Purfleet and Grays Thurrock (Schreve et al., 2002; Roe et al. 2009). Macaques are not found in any later interglacials in Britain, despite the last (MIS 5e, the Ipswichian) being regarded as relatively warm, with the presence of hippo and other thermophilous animals such as the pond terrapin (Candy et al. 2010). However, MIS 5e is notable for the absence in Britain of a number of taxa present in mainland Europe, including *Homo neanderthalensis* and the horse *Equus ferus* (Currant and Jacobi, 2001). Pettitt and White (2012) suggested that the lack of hominins may be explained by the rapid warming at the end of MIS 6, which resulted in

Britain becoming an island very quickly, or because they may not have been adapted to more forested landscapes. While the first may help to explain the lack of *Macaca* in Britain, forest would presumably have been a good habitat for them. Although they are missing from Britain and much of north western Europe in the Late Pleistocene (Figure 3), macaques remained widespread in central and southern Europe until they became extinct. Currently the latest occurrence of *Macaca* in Europe is at Hunas in Germany, dated between 85 ka and 40 ka (Rosendahl et al., 2011). While much of the distribution of fossil mammals in Europe in different interglacials may be due to chance, the presence of *Macaca* in the north during relatively warm periods, and not later, does suggest some level of thermal or behavioural constraint on its dispersal.

The primate day can be divided into four main essential activities: resting, foraging, travelling and socialising (Dunbar, 1988). Highly social and group living, most primates must spend considerable amounts of their day creating and maintaining social relationships, with grooming often being crucial to this effort (Dunbar, 1988). In diurnal species such as macaques, the vast majority (if not the whole) of this activity must be fitted into daylight hours. In the tropics, day and night are of roughly equal lengths and do not vary much throughout the year. In temperate regions, however, there is much more disparity, with considerably shorter days in winter than in summer, resulting in a decline in plant productivity and available food. For the few modern primate species found in temperate regions, these short days impose a dual burden: not only are food resources more scarce or suboptimal, meaning that more time must be spent in foraging or feeding, either to locate food or to gather sufficient quantity to maintain baseline energy needs, but the time available for socialising and keeping groups together is substantially reduced. For example, Japanese macaques inhabiting deciduous forest in winter have been observed to spend the majority of their time (nearly 70%) foraging (Nakagawa, 1989). *Macaca sylvanus* spend more time feeding when there is moderate or heavy snow cover than when snow is absent, possibly because food is of lower nutritional quality in the winter months but also because the increased thermoregulatory demands require concomitant increases in energy intake (Majolo et al. 2013). It has also been demonstrated in southern African baboons that in winter large portions of the relatively short day are spent foraging, and that day length limits group size, bearing in mind that the larger a group, the more time is needed to maintain relationships and hence cohesion within it (Hill et al., 2003).

To investigate the possible constraints on the time budgets of Pleistocene macaques living at relatively high latitudes, we constructed a simple model (Figure 4) tracking daylight during different months of the year at different latitudes and compared these daylight hours to total number of hours of activity during December (the month in which the shortest day falls in the northern hemisphere) in two time-limited modern temperate macaques, non-provisioned *M. fuscata* (Yakushima, day length approximately 10.5 hours in December,: Hanya, 2004) and *M. sylvanus* (Djurdjura and Akfadou, day length approximately 11 hours: Menard and Vallet, 1997). The overall December activity budgets for these northern hemisphere groups were very similar (with around 7.5 hours devoted to socialising, moving and feeding, and around 3 hours to diurnal resting), even though the relative proportions of time devoted to each activity varied slightly . The figures for December are broadly in line with the activity hours recorded for high (southerly) latitude *Papio hamadryas ursinus* in the shortest daylight month, June (Hill et al., 2003).

Differences in the Earth's precession mean that day lengths in the Pleistocene may not have been identical to those today, but our model provides at least an illustration of the magnitude of variation between different latitudes. It indicates that modern temperate macaque December activity minus resting could only just be accommodated in daylight hours at 50°N, so even in the warmer interglacials of MIS 11 and 9 (Pettitt and White, 2012) macaques may have been reaching the geographic limits of ecological tolerance in Britain. If resting time is added, December activity exceeds total day length, but note that monkeys may adjust their activity partly in response to total daylight available. Therefore, the activity hours included in our simple model may thus be an over-estimate of those that are needed for survival. This notwithstanding, the convergence in number of December hours spent travelling, foraging, feeding and socialising in the Yakushima *M. fuscata* group and the Djurdjura and Akfadou *M. sylvanus* groups, below the total number of daylight hours available (Menard and Vallet, 1997; Hanya, 2004), indicates that the figures provide a reasonable winter baseline for essential activity. In regions like Britain with shorter winter days, resting time might be further reduced to allow for essential feeding and socialising. However, given thermoregulatory constraints exacerbated by low food availability on temperate macaques in winter, the costs of foraging and travelling might outweigh feeding returns (Hanya 2004). In *M. sylvanus*, bad winter weather appears to enforce resting (Menard and Vallet, 1997; Majolo et al., 2013). Resting time is therefore vital for conserving energy (Hanya 2004) or even ensuring survival in harsh conditions, and it is unlikely that it could be dispensed with totally.

Socialising is less vital than feeding, even in primates, and might be another area of saving. In monkeys, socialising centres around grooming, and is generally a function of group size

(Dunbar 1988). In December, socialising took around one hour per day in both *M. sylvanus* groups (group size minimum 33, maximum 47; Menard and Vallet, 1997), and approximately two hours in *M. fuscata* (group size ~ 24; Hanya 2004). Assuming that modern *M. sylvanus* provides the best model for its fossil conspecifics, removing its socialising time from the model (to account for the possible effects of very small Pleistocene groups) releases some time constraint, but activity / daylight balance is still marginal (at modern West Runton, there are 7.5 hours of daylight on the shortest day, and activity without resting and socialising is 6.5 hours). In reality, socialising, like resting, cannot be removed altogether. In a recent study of *M. sylvanus* from Morocco, the two most significant predictors of survival after an extremely harsh winter with very high mortality were time spent feeding and number of social relationships (McFarland and Majolo, 2013). This indicates the massive importance of these two factors, and how time can be such a significant ecological constraint for primates (sensu Dunbar et al., 2009).

Group living is vital for primates. Day length has profound effects on temperate primate group size (Hill et al., 2003), but is not the only influence: monkeys must engage in a balancing act to maintain optimal group sizes. Although foraging is the primary activity needed for survival, there needs to be sufficient time remaining for social activity. Thus, maximum ecologically tolerable group sizes may decrease as time constraints increase (Hill et al., 2003). Living in a group inevitably means competing for food with other group members, and according to the Ecological Constraints Model (Chapman and Chapman, 2000), the distribution of food resources also influences primate group size, especially if food is found in patches. In particular, there must be a trade-off between the time it takes for a patch to be depleted (a function of group size) and travelling time to the next patch

(Chapman and Teichroeb, 2012). It has been demonstrated in models of modern primates that this travelling time is a significant ecological factor and may act to limit group sizes (Dunbar et al., 2009). It is therefore possible that these time budgeting constraints would depress group sizes in European macaques to the extent that the minimum viable group size – the number of individuals required to ensure a healthy breeding population – could not be met. This situation is further complicated by the fact that increased predation risk also increases group size (Hill and Dunbar, 1998), so the composition of the ecological community in which fossil macaques lived would exert a separate pressure on group size (Meloro and Elton, 2012) that would also contribute to defining a minimum viable group size.

Maintaining viable group sizes has implications for longer term survival of populations and hence species. Groups do not exist in isolation – in order to promote out-breeding, individuals must move from their natal group. In modern *M. sylvanus*, like the majority of Old World monkeys, females are philopatric and males disperse, although in some populations as many as 50% of the males may stay in their natal groups (Fooden, 2007). Given that *Macaca* was probably not highly abundant in Europe, the loss of marginal groups because of ecological and time pressures may have significantly reduced the genetic diversity of the species in the region due to inbreeding, as males would be forced to remain in their original group, as is seen in some modern populations. This may have been compounded by climatic fluctuations forcing populations into refugia. It has been argued that survival of large carnivorans in the European Pleistocene may have been compromised by chance evolutionary events in small refugial populations (O'Regan et al., 2002). Small refugial macaque populations would similarly have been at risk of extinction because of stochastic genetic factors, such as bottlenecks, preventing viable groups re-emerging (Meloro and Elton, 2012). Environmental stochasticity and decreased genetic diversity are significant causes of extinction in modern organisms (Lande, 1993, 1998), and it is easy to see how these factors could push European macaque populations below minimum viable size. Other factors that influence group size – and may tip a population and ultimately a species from viability to inviability - are reproductive and mortality rates (Lande, 1993; Melbourne and Hastings, 2008), which in turn are affected by climate.

4. Modelling distributions: the influence of climate

Several modern macaque species, including *M. mulatta*, *M. fuscata* and *M. sylvanus*, exploit relatively high latitude and / or high altitude environments, exposing them to temperature extremes that are rarely experienced by tropical primates. The non-human primate with the most northerly modern distribution is *M. fuscata*, the Japanese macaque. Found at latitudes as far north as 41°, the 'snow monkey' is well known for surviving in relatively harsh winter conditions. At one of the most northerly *M. fuscata* study sites, Kazamaura on Honshu (41°N), the temperature can dip to -6°C in the winter and rise to 26°C in the summer, with mean temperatures ranging through the year from -2.5°C to 22°C (data taken from http://en.climate-data.org/location/472551/). *M. mulatta*, found in the Chinese Taihang Mountains and the Himalayan foothills of India and Pakistan, also experiences temperatures that drop to below freezing during the winter (Qu et al., 1993; Goldstein and Richard, 1989). At Midelt, in the High Atlas, *M. sylvanus* individuals may experience annual temperatures that fluctuate from -10°C in the winter to +33°C in the summer (data from http://en.climate-data.org/), and exploit environments that are snow bound during parts of the year (Fooden 2007). As discussed above, dietary strategy and foraging behaviours help modern macaques survive, as do social relationships (McFarland and Majolo, 2013). Balancing different demands in marginal environments can be challenging for temperate primates. For instance, notwithstanding the increased difficulties finding food in the winter, when the temperature was very low, feeding and travelling time in *M. fuscata* dropped because of the need to conserve energy for thermoregulation (Hanya, 2004). Variation in rainfall can also pose challenges for temperate primates: during the summer dry season *M. sylvanus* foraging effort increases and social interaction decreases (Menard, 2002). Climate also has a profound effect on other aspects of primate lives, including changes to reproductive rate: slower reproduction in *M. fuscata*, for example, aids mothers to better ensure the survival of their offspring in harsh conditions (Wolfe, 1986), although slow reproductive rates can have enormously detrimental effects on population size and survival, especially if they are coupled, as seen recently in modern *M. sylvanus* (McFarland and Majolo, 2013), with higher than average mortality.

The responses to climate discussed here are socioecological fundamentals observed across the primate order, and would be expected to occur in extinct *M. sylvanus* under similar environmental conditions. Surprisingly little has been written about the types of environments exploited by European macaques in the Pliocene and Pleistocene. Based on climate simulations for 3 Ma, Pliocene Europe - particularly at the higher latitudes - was warmer than the present (possibly by up to 5°C) and probably wetter and less seasonal (Haywood et al., 2000). The Pleistocene brought cooler and drier conditions, with greater climatic fluctuation (Zachos et al. 2001). Nonetheless, during some warm phases up to and including the Middle Pleistocene, the climate of ‘marginal’ areas such as Britain are likely to have been warmer than today and have even been compared to the modern Mediterranean

(Parfitt et al., 2005). It has been suggested that the *M. sylvanus* teeth recovered from Hoxne are stratigraphically associated with lemmings, viewed today as a cold climate animal, and hence that some Pleistocene macaques may have inhabited a relatively harsh environment (Singer et al., 1982). However, more recent work (Ashton et al., 2008) has highlighted the complexity of the assemblages at Hoxne, tracking the fluctuating climate of MIS 11. Beetles from stratum C, for example, indicate a cold climate (with temperatures likely to be as low as -10°C in the winter and reaching a July maximum of around +10°C), whereas pollen from the older stratum E indicate temperate (rather than cold climate) deciduous woodland (Ashton et al., 2008). The macaque fossils, recovered from stratum B, are associated with a warm fauna comprising lion, red, roe and fallow deer, bear, horse, and extinct rhinoceros, as well as extinct giant beaver and lemming (Ashton et al., 2008). Based on analogy with modern-day fauna, the presence of lemming seems incongruous. However, they have been found at other Middle Pleistocene sites with deciduous woodland, such as Boxgrove, and just as the distribution of the larger fauna such as lion has changed over time, lemming distribution and habitat preferences may also have shifted (Ashton et al., 2008). It is also possible that the specimens are *Myopus* (wood lemming) rather than *Lemmus* (true or Norway lemming), adding weight to the reconstruction of a more boreal rather than cold environment (Schreve, 2012). Although macaques have not been recovered from Boxgrove (MIS 13), palaeotemperature reconstruction based on ostracod environmental tolerances suggests a summer high of around 20°C and a winter low of -4°C (Holmes et al., 2010), within the tolerance of modern *M. sylvanus* and *M. fuscata*.

When reconstructing the distributions of past species, now either totally extinct or extinct in a particular area, the fossil record is inevitably the primary source of data, subject to the usual challenges of taphonomic bias and incomplete preservation. However, since findspots are unlikely to replicate exactly the actual distribution of a given species, it can be useful to employ models. Although models are at best an approximation, and are unlikely to incorporate all the parameters that influence the geographic range of a species, they have heuristic and exploratory value. For example, they may help in the formulation of new hypotheses that can be empirically tested or provide context that may direct future avenues of research. For species with known or well-reconstructed environmental preferences and tolerances, it is possible to explore dispersals using programs such as ‘Stepping Out’ (see for example Hughes et al., 2008), although the accuracy and resolution of such models are dependent on the quality of available palaeoenvironmental data. Another approach is to predict the geographic range or distribution of an extinct species, rather than the act of dispersing itself, using ecological niche modelling techniques developed for modern biodiversity assessment. These models, constructed using known fossil findspots in conjunction with environmental data, including temperature, precipitation, vegetation and elevation have been used to explore the potential ranges of various extinct organisms (Waltari et al., 2007; Maguire and Stigall, 2009; Elton and Dunn, in press) but have never to our knowledge been used with non-hominin fossil primates. We thus modelled possible distributions for *M. sylvanus* across Europe and North Africa at three points in time (the last Pleistocene interglacial, the last glacial maximum and today). We ran the models in DIVA-GIS using the BIOCLIM/DOMAIN ‘Predict’ tool (Hijmans et al. 2012), employing fossil findspots (Table 2) and environmental data based on their geographic coordinates to train the model, which are then used to predict probability of occurrence for a wider modelled area.

Like all models, those developed for range prediction are dependent on the quality of the underlying data. Many different lines of evidence (including global-scale dust and oxygen isotope records from deep sea and ice cores, regional-scale pollen and faunal evidence and local scale palaeosol data) have contributed to what is known about Pleistocene climates in the Old World (Elton, 2008). However, as past climates and environments were highly variable spatially as well as temporally (Trauth et al., 2009), with inherent challenges moving from global to regional to local scales of evidence (Elton, 2008), the environmental data used in the distribution modelling were kept as simple as possible to offset error caused by over-interpretation or extrapolation. Well validated climatic data are available from the WORLDCLIM database (Hijmans et al., 2005) for the three time periods of interest and we thus used WORLDCLIM bioclimatic (BIOCLIM) variables relating to mean annual precipitation and temperature, as well as maximum and minimum temperatures, in our models. Mean annual precipitation (BIO12) and mean annual temperature (BIO1) have been shown in previous primate models to be important predictors of occurrence (Dunbar and Korstjens, 2008; Korstjens et al. 2010), while other studies have indicated that temperature variation or seasonality, rather than annual temperature per se, are critical factors that limit primate distributions (Lehmann et al. 2008; Bettridge et al. 2010). In addition, although modern *M. sylvanus* can survive in relatively cold areas, higher mortality is reported during very cold winters (McFarland and Majolo, 2013). Thus, minimum temperature of the coldest month (BIO6) and maximum temperature of the warmest month (BIO5) were also included in the models.

For the last interglacial (LI) model, climate data derived by WORLDCLIM using modern data downscaled according to parameters reported in Otto-Bliesner et al. (2006) and provided at a resolution of 30 arc seconds (roughly 1 km^2) were used. The WORLDCLIM Community Climate System Model (CCSM) dataset for the last glacial maximum (LGM), derived from PMIP2 (Braconnot et al., 2007) and provided with a lower resolution of 2.5 by 2.5 arc minutes (equivalent to approximately 25 km^2 in area at the Equator), was used in the LGM model. The modern WORLDCLIM BIOCLIM data, also at a resolution of 2.5 arc minutes, were used in the model of expected distribution today. Given the broad similarities in topography between the Late Pleistocene and the Holocene, modern elevation data (taken from WORLDCLIM) were used for all models. The resulting modelled distributions are illustrative, and as the resolution of the LI is higher than that of the LGM and modern models, they are not directly comparable.

Two LI models were constructed, the first using fossil findspots from the Middle Pleistocene (0.78-0.12 Ma) and the second using only fossil findspots from the Late Pleistocene. DIVA-GIS distribution models predict probability of occurrence on a scale from 'excellent = red' to 'not suitable = grey' (Hijmans et al. 2012), and the LI model based on the Middle Pleistocene data predicted excellent to high probability of occurrence in western Europe and the Thames region of Britain, and medium probability in parts of northern and central Europe and some regions of North Africa and Iberia (Figure 5A). The LI model based on Late Pleistocene findspots predicted excellent to high probability of occurrence only in parts of Iberia, North Africa, southern, western and central Europe but a nil probability in Britain (Figure 5B).

Possible macaque distributions in the LGM were modelled using Late Pleistocene fossil findspots (Fig. 6A) and also with only modern North African sites (Fig. 6B). The LGM / Late

Pleistocene model (Fig. 6A) gives a very high or excellent probability of occurrence in western, central and southern Europe, including Iberia, but a nil probability in Britain. There was a very high or excellent yet slightly patchy occurrence probability in North West Africa. Using the same fossil findspots, the LGM models appear to predict a slightly more extensive distribution than the LI, probably an artefact of the different resolutions of the models. In the LGM model that included only modern North African sites, there was an excellent to high predicted probability of occurrence in south and west Iberia and parts of North Africa, with probability of occurrence in very limited areas of Greece and the eastern Mediterranean (Fig. 6B).

The patchiness of predicted occupation in North Africa in both Pleistocene models (LGM and LI) is interesting in the light of molecular data that suggest that North African *M. sylvanus* populations are not monophyletic, with a split around 1.6 Ma between a clade comprising the Moroccan specimens and the Algerian population from Kherrata and a clade comprising the remaining Algerian populations (Modolo et al., 2005). This was followed by further subdivision between the groups in the Late Pleistocene (Modolo et al., 2005). It is possible that climate, driving regional differences in vegetation or vicariance, contributed to differentiation within North African macaques.

Given that modern *M. sylvanus* is locally extinct in Europe, range contraction or extirpation must have occurred at some point in the Late Pleistocene or Holocene. However, the evidence from the fossil record (Figure 3 and Supplementary Information) suggests that the retreat into the modern range did not occur until well into the Late Pleistocene. One possible explanation for the range contraction experienced by *M. sylvanus* is climate change between the Late Pleistocene and today, and ecological niche and species range prediction models based on modern data were used to explore this. Occurrence sites of extant *M. sylvanus* (Supplementary Information) without Gibraltar were used in the modern model. There was an excellent, very high or high probability of occurrence in modern North Africa, central and southern Spain, coastal Italy, Sicily, Sardinia and around the Aegean (Fig. 7). Although the climate-based models incorporate only a selective number of variables (with no inclusion of factors related to community dynamics), the indication that modern *M. sylvanus* could inhabit much of southern Europe is anecdotally supported not only by the semi free-ranging modern population that exists on Gibraltar but also by the thriving captive provisioned yet exclusively outdoor colonies further north at wildlife parks in the UK, France and Germany. There is an implicit assumption that *M. sylvanus* survives in North Africa because it originated there, bolstered by suggestions that North Africa acted as a refuge during glacial cycles (Modolo et al. 2005). Yet North Africa may have been a no more likely refuge for a largely continental European-distributed species than other probable refugia such as Spain or Italy.

One clear limitation of our modelling, because of the lack of a high resolution pan-European Pleistocene dataset, is a failure to consider the effects of biome or vegetation. The climate data that we include in the models are likely to be linked closely to vegetation, but if we assume that *Macaca* was patchily distributed and not very abundant, small vegetation differences within or between regions could have a profound influence on dispersal and distribution. Future work on European fossil macaques that includes directly-reconstructed palaeobiological and palaeoenvironmental data may help to explore these effects more fully. Similarly, the presence or absence of ‘microrefugia’ suitable for macaque exploitation may have had a significant impact on the survival and distribution of the genus, and this topic is also ripe for investigation. Another notable omission from the work we present here is a thorough consideration of how competition, predation pressure and community dynamics may have influenced macaque dispersal and distribution across Europe, including consideration of the biogeography and evolutionary patterns seen in other monkeys and large mammals. This notwithstanding, our climate (and time budget) models provide a first, hopefully informative, step in understanding the biogeographic history of *M. sylvanus*.

5. *Macaca sylvanus* – a forgotten late Pleistocene extinction?

The longevity of *Macaca* in Europe during the Pliocene and Pleistocene, and ultimately its extinction, makes it a possible candidate for inclusion in the Late Quaternary faunal turnovers. While the loss of the larger, perhaps more charismatic megafauna such as the mammoth, lion and hyaena have attracted much study and debate, the demise of Europe's only non-hominin primate has gone largely unremarked. Based on current evidence it joins *Hippopotamus amphibius* (the hippo), *Palaeoloxodon antiquus* (the straight-tusked elephant) and *Stephanorhinus hemitoechus* (narrow-nosed rhinoceros) in becoming extinct in the first half of the last glacial (reviewed in Stuart and Lister, 2010). Both *P. antiquus*, warm-temperate and forest-adapted, and *S. hemitoechus*, a browser, may have gone extinct, around or slightly later than the extinction date postulated for the Barbary macaque in Europe, because the lowering of global and regional temperatures in the last glacial period caused reduction in forest cover. It is plausible therefore that the same set of factors may help to explain the extinction of *Macaca* in Europe.

Another plausible factor is the influence of hominins. Currently it seems that macaques may have become extinct before the arrival of modern *Homo sapiens* in Europe (dated to between 45 and 43 kya in southern Europe (Benazzi et al., 2011) and over 41 kya in north-western Europe (Higham et al., 2011)) but this is not certain, given the scarcity of Late Pleistocene macaque material. However, they must have co-existed alongside earlier *Homo* species for over 1 million years (Oms et al, 2000; Toyo-Moyano et al., 2013), with macaques and hominins found at a number of Early and Middle Pleistocene sites including Cueva Negra del Estrecho del Quípar and Solana del Zamborino in Spain, and Galeria Pesada in Portugal (see Marigó et al., in press). Evidence of hominins (both fossils of *H. neanderthalensis* and/or stone tools) is also present with *Macaca* (although not always within the same levels) at a number of Late Pleistocene sites, including Hunas (Rosendahl et al., 2011), Grotta degli Orsi Volanti (Mazza et al., 2005), Kugelsteinhöhle II (Fladerer, 1991), Cova Negra (Marigó et al., in press) and Lezetxiki (Castanos et al., 2011). Modern ecological studies indicate that Barbary macaques do not live comfortably alongside humans, and unlike baboons, vervets and some Asian macaques, do not exploit human habitats (Menard, 2002). Human occupation is a highly significant negative influence on modern *M. sylvanus* distributions (Menard, 2002; Butynski et al., 2008). Given the association between fossil macaques and *Homo* in the Late Pleistocene fossil record – and bearing in mind the long history of hominin predation on monkeys, including the threat that the contemporary bushmeat trade poses to extant primates - it is highly likely Pleistocene macaques fell prey to *Homo*, especially in resource-limited environments (Meloro and Elton, 2012). Predation by *Homo* therefore cannot be discounted as a contributing factor in macaque extinction in Europe (Meloro and Elton, 2012).

6. Conclusions

We set out to explore the biogeography and extinction of European macaques. Macaques are very widely distributed in Europe throughout the Pliocene and Pleistocene, with the British *Macaca* specimens being among the most northerly post-Eocene euprimates ever recorded. Our time budget model indicates that at higher latitudes winter day length would have been a significant constraint on sociality and foraging. Although macaques were likely to have been highly ecologically flexible, group sizes in some areas may have been depressed to below the minimum viable group size by poor resource availability (determined by climate and daylight), the ability to procure this food (determined by daylight) and the lack of time necessary to maintain large enough social groups to provide protection against predators (determined by daylight and time constraints imposed by travelling and foraging time).

Pliocene and Pleistocene *M. sylvanus* could probably have inhabited both deciduous and coniferous forest, and may also have been able to exist in some of the transitional environments that occurred going into or coming out of glaciations. Our climate models suggest the potential for relatively extensive distribution in Europe, including areas where no fossils are currently recorded (including much of northern and central France, where currently there is only one findspot (Limondin-Lozouet et al., 2010), during the Middle and Late Pleistocene. They further indicate that although *Macaca* is now absent, the climate in parts of present-day Europe may still be suitable for its survival, although further work is required to assess fully the impacts of vegetation change. The extinction of European *Macaca* in the Late Pleistocene is coincident with the loss of other large-bodied woodland-adapted taxa such as *Palaeoloxodon antiquus* and *Stephanorhinus hemitoechus*, which could relate to climate-induced vegetational changes. However, given the presence of hominin fossils or artefacts at several sites that also record *Macaca* in the Late Pleistocene, we cannot rule out that the activities of *Homo* may have ultimately contributed to the demise of *Macaca* in Europe.

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Table

Table 1. Area of distribution for modern Macaques and European fossil macaques based on modern ranges (IUCN, 2013) and Pleistocene fossil findspots (see Supplementary Information). Polygons calculated in QGIS (2013). The Pliocene distribution was more-or-less circum-Mediterranean so no range was calculated for that period.

Species	Time period	Region (sites) included in polygon	Polygon area (km^2)
M. mulatta	Modern	Whole species range	6,647,129
M. fascicularis	Modern	Whole species range	2,230,482
M. assamensis	Modern	Whole species range	1,583,128
M. leonine	Modern	Whole species range	1,291,321
M. arctoides	Modern	Whole species range	1,229,367
M. thibetana	Modern	Whole species range	1,188,736
M. nemestrina	Modern	Whole species range	1,120,531
M. radiate	Modern	Whole species range	521,473
M. fuscata	Modern	Whole species range	147,195
M. tonkeana	Modern	Whole species range	66,653
M. sinica	Modern	Whole species range	38,295
M. ochreata	Modern	Whole species range	35,327
M. cyclopis	Modern	Whole species range	23,555
M. silenus	Modern	Whole species range	23,178
M. hecki	Modern	Whole species range	19,655
M. nigrescens	Modern	Whole species range	8,003
M. nigra	Modern	Whole species range	6,281
M. maura	Modern	Whole species range	3,932
M. siberu	Modern	Whole species range	3,165
M. pagensis	Modern	Whole species range	1,755
M. munzala	Modern	Whole species range	1,535
M. sylvanus	Modern	Whole species range	38,613
M. sylvanus	Late Pleistocene	Europe	1,292,853
M. sylvanus	Middle Pleistocene	Europe without Caucasus	2,352,144
M. sylvanus	Middle Pleistocene	Europe with Caucasus	3,756,694
M. sylvanus	Early Pleistocene	Europe without Caucasus	1,845,609
M. sylvanus	Early Pleistocene	Europe with Caucasus	2,229,377

Figures

Figure 1. Temporal ranges of non-hominin primates in Europe.

					0.01	Modern
				▨	0.13	Late Pleistocene
			▨	▨	0.8	Middle Pleistocene
		▨	▨	▨	1.8	Early Pleistocene
▨	▨	▨		▨	3.6	Late Pliocene
▨	▨			▨	5.3	Early Pliocene
▨				▨	~6	Latest Miocene
Mesopithecus	***Dolichopithecus***	***Paradolichopithecus***	***Theropithecus***	***Macaca***	**Millions of years ago**	**Epoch**
Present in Europe						

Figure 2: Fossil *Macaca* findspots in Europe, North Africa and Caucasus from the Miocene to the Early-Middle Pleistocene boundary. (Not all Miocene *Macaca* sites in North Africa shown.)

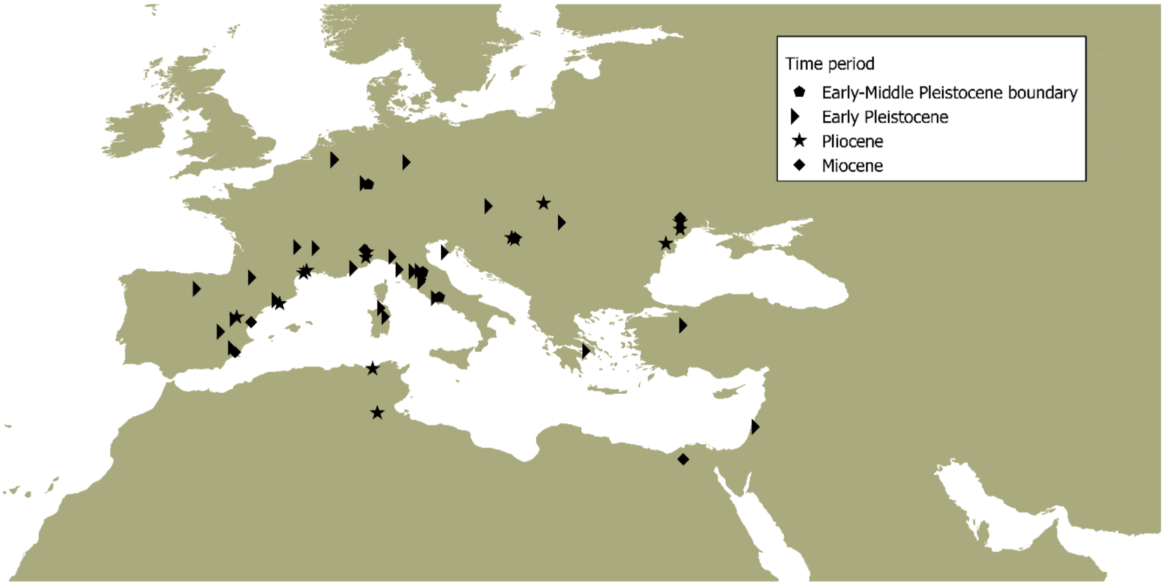

Figure 3: Fossil *Macaca* findspots in Europe, North Africa and Caucasus in the Middle and Late Pleistocene.

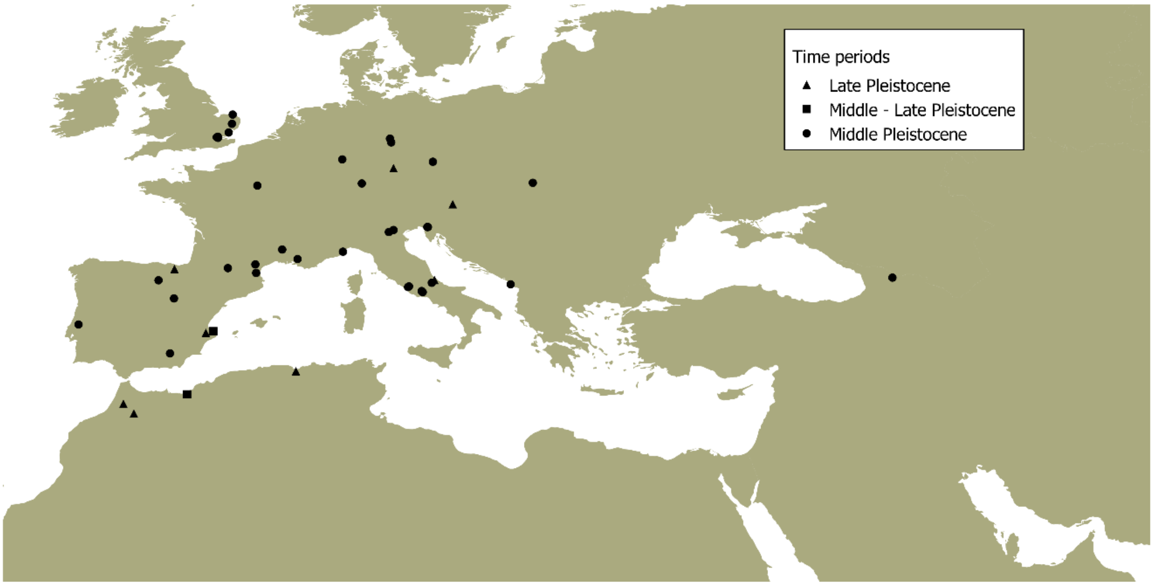

Figure 4: Time budget model showing hours of activity (socialising, feeding, foraging, moving, resting) in December for temperate macaques (*M. sylvanus*, Barbary macaque [data from Menard and Vallet, 1997] and non-provisioned *M. fuscata*, Japanese macaque [data from Hanya 2004]) alongside hours of daylight at latitudes from 30°N to 60°N.

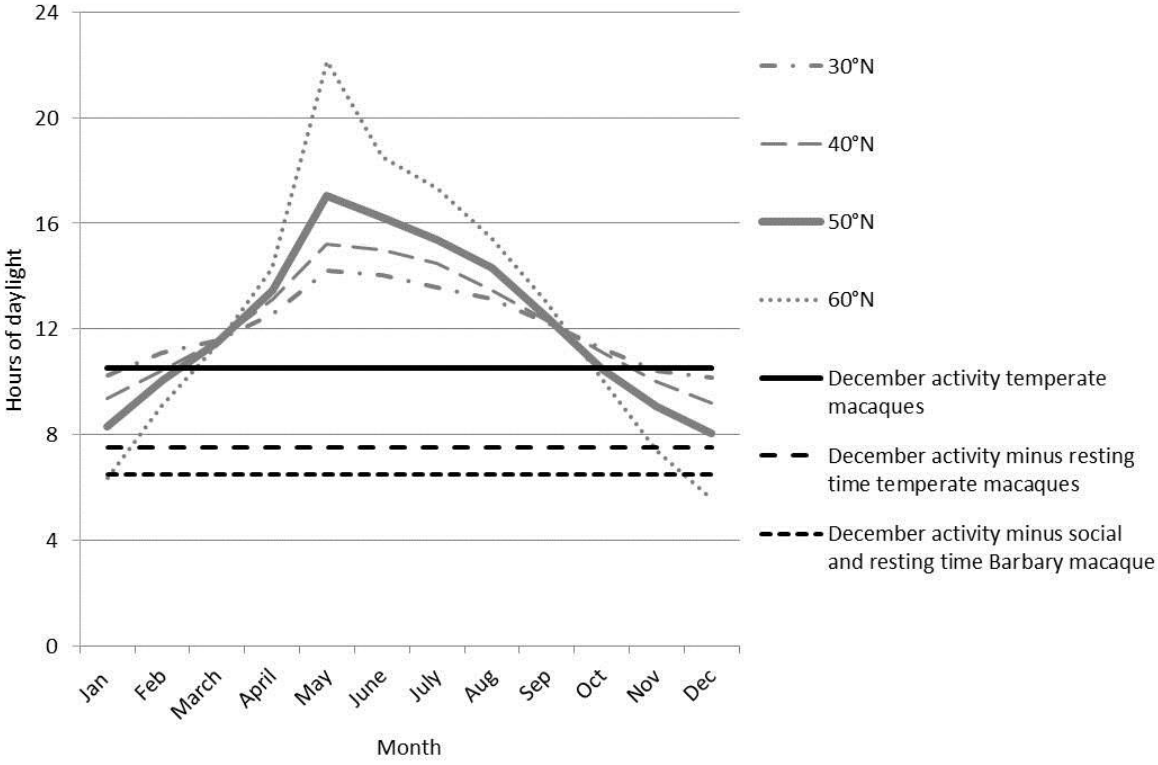

Fig. 5. Results of model using Last Interglacial climate (at a resolution of 30 arc seconds) with (A above) Middle Pleistocene fossils and (B below) Late Pleistocene fossils. Note that Figure 5 is not directly comparable with Figures 7, 8 and 9 because of differences in the resolution of the underlying climate data.

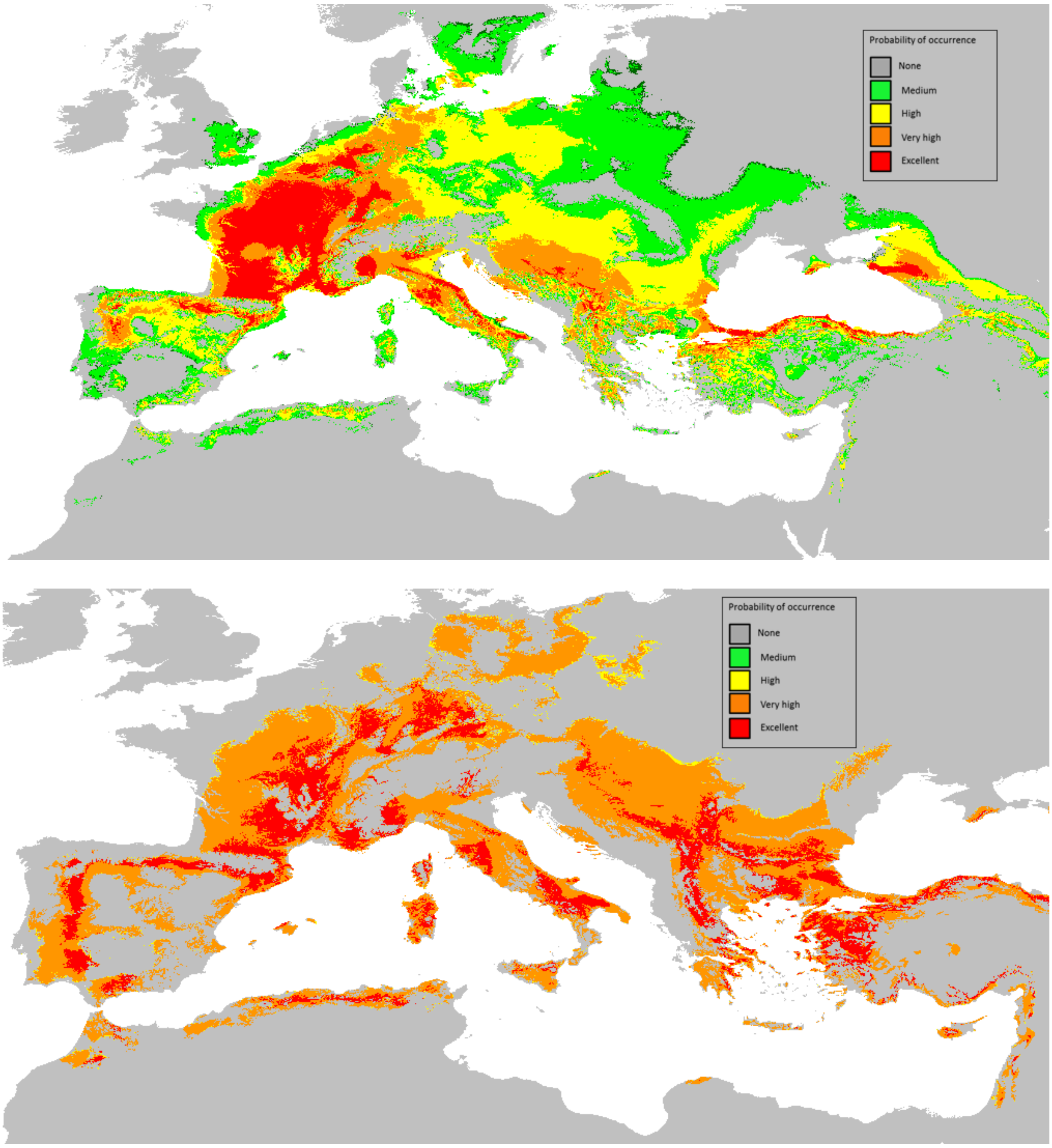

Fig 6. Results of model using Last Glacial Maximum climate (at a resolution of 2.5 arc minutes) with (A top) Late Pleistocene fossils and (B below) modern data. Note that Figures 6 and 7 are directly comparable but are not directly comparable with Figure 5 because of differences in the resolution of the underlying climate data.

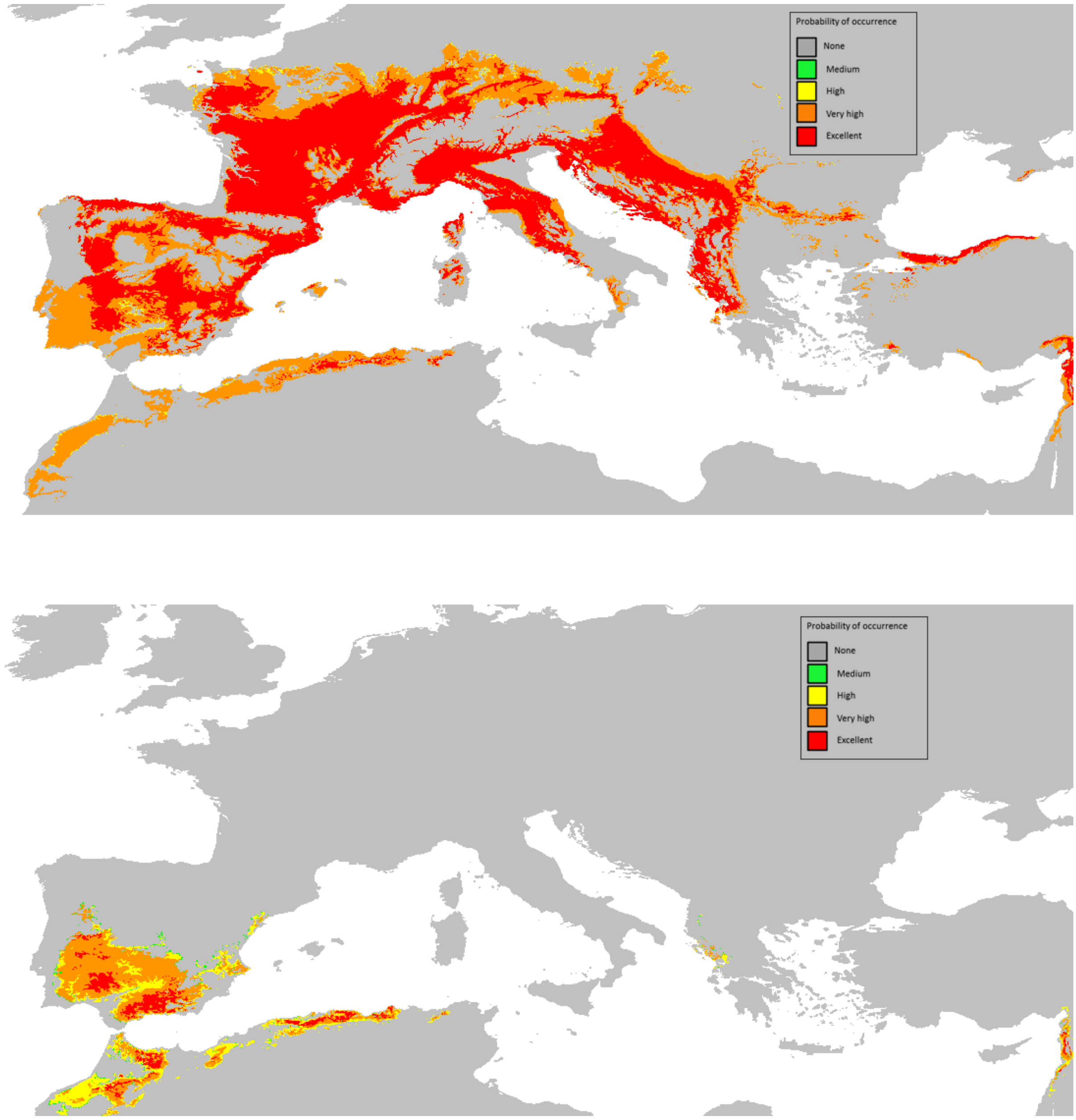

Fig 7. Results of model using modern climate (at a resolution of 2.5 arc minutes) with modern data (not including Gibraltar). Note that Figures 6 and 7 are directly comparable but are not directly comparable with Figure 5 because of differences in the resolution of the underlying climate data.