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Late Pleistocene human population bottlenecks, volcanic winter, and differentiation of modern humans

The "Weak Garden of Eden" model for the origin and dispersal of modern humans (Harpending *et al.*, 1993) posits that modern humans spread into separate regions from a restricted source, around 100 ka (thousand years ago), then passed through population bottlenecks. Around 50 ka, dramatic growth occurred within dispersed populations that were genetically isolated from each other. Population growth began earliest in Africa and later in Eurasia and is hypothesized to have been caused by the invention and spread of a more efficient Later Stone Age/Upper Paleolithic technology, which developed in equatorial Africa.

Climatic and geological evidence suggest an alternative hypothesis for Late Pleistocene population bottlenecks and releases. The last glacial period was preceded by one thousand years of the coldest temperatures of the Later Pleistocene (~71–70 ka), apparently caused by the eruption of Toba, Sumatra. Toba was the largest known explosive eruption of the Quaternary. Toba's volcanic winter could have decimated most modern human populations, especially outside of isolated tropical refugia. Release from the bottleneck could have occurred either at the end of this hypercold phase, or 10,000 years later, at the transition from cold oxygen isotope stage 4 to warmer stage 3. The largest populations surviving through the bottleneck should have been found in the largest tropical refugia, and thus in equatorial Africa. High genetic diversity in modern Africans may thus reflect a less severe bottleneck rather than earlier population growth.

Volcanic winter may have reduced populations to levels low enough for founder effects, genetic drift and local adaptations to produce rapid population differentiation. If Toba caused the bottlenecks, then modern human races may have differentiated abruptly, only 70 thousand years ago.

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Introduction

Several alternative models for the origin of modern human races are currently being debated by paleoanthropologists (Aiello, 1993; Lahr, 1996). Regional Continuity (Multiregional Evolution) and hybridization models (Afro-European *sapiens* and Assimilation) are based largely on interpretations of fossil evidence. Three variations on the theme of a recent African origin for modern

humans (Replacement, Weak Garden of Eden and Multiple Dispersals) are based on combinations of evidence from fossils, archaeology, paleobiogeography, paleoclimatology and the genetic structure of extant human populations. The main purpose of this paper is to evaluate and explain one component of the Weak Garden of Eden (GOE) model (Harpending *et al.*, 1993; Sherry *et al.*, 1994; Rogers & Jorde, 1995). The Weak GOE assumes a late

Middle Pleistocene African origin for modern humans (Cann *et al.*, 1987; Stoneking *et al.*, 1992), subdivision and dispersals of populations during the early Late Pleistocene, followed by dramatic reduction (bottlenecks) and expansion (releases) in population size in each region. Population growth after the bottlenecks is related to the invention and spread of modern human technology (the Upper Paleolithic or Later Stone Age) during the latter half of the Upper Pleistocene. This paper presents an alternative hypothesis: volcanic winter resulting from the super-eruption of Toba (Sumatra) caused the bottleneck and populations expanded before the advent of modern technology. If this hypothesis is correct, modern human races differentiated abruptly, mainly through the founder effect, genetic drift and adaptation to local environments, only 71–70 ka (thousand years ago).

Competing models for the origin of modern humans

Regional Continuity and Hybridization models

The Regional Continuity or Multiregional Evolution model (Wolpoff, 1989) proposes that populations of *Homo erectus* dispersed from Africa throughout the Old World about 1.0 m.y.a. and evolved into modern humans in each region. Gene flow between regions prevented speciation and carried all regional populations across the threshold of modern humanity in close synchrony, while allowing regional population characters to evolve. New dates on fossils of *Homo erectus* from Java, southern China and Georgia suggest hominid dispersal occurred about 1.8 m.y.a. (Swisher *et al.*, 1994; Huang *et al.*, 1995; Gabunia & Veuka, 1995; Larick & Ciochon, 1996). If these dates are confirmed, modern human geographic differentiation in the Multiregional model would have begun 1.8 m.y.a.

Two variants of the Regional Continuity model suggest African immigrants played a more important role in modern human origins outside of Africa, particularly in western Eurasia. The Afro-European *sapiens* or Hybridization and Replacement hypothesis (Bräuer, 1992) posits a large African contribution to modern human populations via hybridization with, and assimilation of, Africans in Europe and western Asia. The African Assimilation model (Smith, 1992) proposes a smaller African genetic contribution to modern human populations in Europe and West Asia, by assimilation of small numbers of African immigrant genes.

Replacement models

Out of Africa in the Later Pleistocene. The Noah's Ark (Howells, 1976), Replacement (Stringer & Andrews, 1988), Strong Garden of Eden (Harpending *et al.*, 1993), African Eve (Cann *et al.*, 1987) or Out of Africa (Giles & Ambrose, 1986) model suggests that anatomically modern African populations originated sometime in the last 140–200 ka (Cann *et al.*, 1987; Stoneking *et al.*, 1992) and completely replaced archaic ones outside of Africa sometime during the last 100,000 years. Regional variants of the descendants of *Homo erectus*, known as "Archaic" *Homo sapiens* (*H. heidelbergensis*), including their neanderthal descendants in western Eurasia, made no genetic contribution to modern humans (Krings *et al.*, 1997). Proponents of Replacement note that the earliest modern and near-modern human fossils occur throughout Africa 100–250 ka, long before they appear elsewhere (Bräuer, 1992; Bräuer *et al.*, 1997; Stringer & Andrews, 1988). The earliest truly anatomically modern humans outside of Africa are found on Africa's doorstep, in the Levant, and date to about 100 ka (Stringer & Andrews, 1988).

The dispersal date of around 100 ka is important because it suggests that modern humans left Africa during oxygen isotope

stage 5, the generally warm, humid last interglacial period, ~130 to ~74 ka (chronology of isotope stages after [Martinson *et al.*, 1987](#)). [Tchernov \(1992a, 1992b\)](#) has compiled an impressive body of paleontological evidence demonstrating that African hominids were members of an Afro-Arabian biotic community that expanded northward and out of Africa across the Sinai Peninsula to the southern Levant during stage 5. This was only the latest of several such multi-species dispersals out of Africa during warm and humid interglacial phases. During cold glacial periods, including oxygen isotope stages 6 and 4 (~190–130 and ~74–60 ka, respectively), cold and arid-adapted Palearctic biotic communities returned to southwest Asia ([Tchernov, 1992a, 1992b](#)).

Genetic evidence for a recent African, rather than an ancient Multiregional origin for modern human populations, was first clearly demonstrated by [Lewontin \(1972\)](#). He showed that total human genetic diversity is extremely low (though highest in Africa) and most is contained within populations in each geographic region. Twenty-five more years of genetic research have provided additional support for Lewontin's observation that only ~10% of human genetic variation is accounted for by differences between populations ([Relethford, 1995](#)). Humans also have extraordinarily low level of within- and between-population genetic variation in comparison to great apes ([Ferris *et al.*, 1981](#); [Ruvolo *et al.*, 1993](#)), further supporting an extremely recent origin for modern humans.

Mitochondrial DNA base sequence data reinforce the Replacement model. [Cann *et al.* \(1987\)](#) showed that Africans have much greater mtDNA diversity than European and Asian populations and inferred that all non-African populations can be traced back to an African "Eve" who may have lived about 140–200 ka ([Cann *et al.*, 1987](#); [Vigilant *et al.*, 1991](#); [Horai *et al.*, 1995](#); [Ruvolo *et al.*, 1993](#); [Stoneking *et al.*,](#)

[1992](#); [Stoneking, 1993](#)). Non-African populations have roughly half the genetic diversity and thus seem to be no older than half this age (assuming amounts of genetic difference are proportional to time), indicating a more recent origin for non-African modern populations, about 100 ka. This interpretation has been challenged by [Templeton \(1993, 1996\)](#), but improved strategies of analysis of large data sets have surmounted many of these problems ([Penny *et al.*, 1995](#)). [Rogers & Jorde \(1995\)](#) argue Templeton's method of analysis is unlikely to work well in populations that have undergone rapid size expansions. The effects of different population sizes and amounts of gene flow on population genetic diversity and on phylogenetic reconstructions pose far more substantial problems for an African origin of modern humans ([Relethford, 1995](#); [Relethford & Harpending, 1995](#)). However, an African origin for modern humans receives additional support from Y chromosome ([Hammer & Zegura, 1996](#); [Hammer *et al.*, 1997](#)) and nuclear DNA research ([Wainscoat *et al.*, 1986](#); [Cavalli-Sforza *et al.*, 1988, 1994](#); [Goldstein *et al.*, 1995](#); [Ayala & Escalante, 1996](#); [Ayala, 1996a, 1996b](#); [Tishkoff *et al.*, 1996](#); *contra* [Wolpoff, 1996](#); [Templeton, 1996](#)) and is consistent with the fossil record (see below).

If the Regional Continuity, Afro-European *sapiens* Hybridization or Assimilation models ([Wolpoff, 1989](#); [Bräuer, 1992](#); [Smith, 1992](#)) were correct, one would predict at least a few intra-regionally distinctive widespread alleles in non-African populations that cannot be traced to recent African populations ([Stoneking, 1993](#); [Manderscheid & Rogers, 1996](#); [Rogers, 1995](#)), especially if regional populations were established as early as 1.8 m.y.a. For example, if neanderthals contributed to the gene pool of modern western Eurasians they should now express a unique suite of distinctive alleles. However, ancient non-African alleles have not yet been found

(Tishkoff *et al.*, 1996; Hammer *et al.*, 1997; Manderscheid & Rogers, 1996) and neanderthal mtDNA differs substantially from that of living humans (Krings *et al.*, 1997).

Craniometric variation, when analyzed in a fashion analogous to that of the genetic composition of modern humans by Lewontin (1972), provides remarkably similar results (Relethford, 1994; Relethford & Harpending, 1994). Craniometric variation within geographic populations is far greater than between them and differences between populations are small. Waddle's (1994) analysis of craniometric variation in fossil hominids also demonstrates a high degree of similarity among anatomically modern Upper Pleistocene individuals between regions, as well as similarity to late Middle Pleistocene Africans, thus supporting an African origin for Upper Pleistocene modern humans. Neanderthals appear to be substantially different in mtDNA (Krings *et al.*, 1997) and morphology from other hominids (Schwartz & Tattersall, 1996), have chronological overlap with modern humans in Europe (Hublin *et al.*, 1996) and show no special morphological relationship to western Eurasian modern humans (Waddle, 1994; Turbón *et al.*, 1997; Holliday, 1997). If the Multiregional model is correct, then Upper Pleistocene and modern humans from each region should differ from those of other regions as much as neanderthals differ from modern humans (Waddle, 1994). Indeed, if southeast Australasian populations left Africa 1.8 m.y.a. (Larick & Ciochon, 1996), they should have evolved a much more pronounced suite of regionally distinct morphological characters than those of neanderthals, whose ancestors first permanently occupied western Eurasia only 500 ka (Rightmire, 1997). If the Upper Pleistocene age of advanced *Homo erectus* from Ngandong, Java, is confirmed (Swisher *et al.*, 1996), it is consistent with Waddle's (1994) observations and incompatible with Regional Continuity.

The Multiregional model and its variants appear to be wholly incompatible with fossil, genetic and craniometric evidence described above. In the remainder of this paper variants of the Replacement model are considered more accurate and realistic accounts of the origin and spread of modern humans.

Replacement models with bottlenecks

Several studies of nuclear and mitochondrial DNA have identified a significant bottleneck or bottlenecks (reductions in population size) followed by substantial population growth (release), sometime during the last glacial period (Haigh & Maynard Smith, 1972; Jones & Rouhani, 1986; Cann *et al.*, 1987; di Rienzo & Wilson, 1991; Harpending *et al.*, 1993; Sherry *et al.*, 1994; Rogers & Jorde, 1995; Takahata, 1993; Takahata *et al.*, 1995; Templeton, 1993; Watson *et al.*, 1997; Bortoline *et al.*, 1997). Detailed explanation of the methods by which population bottlenecks are identified is beyond the scope of this discussion, but are well-described in the current literature (di Rienzo & Wilson, 1991; Harpending *et al.*, 1993; Marjoram & Donnelly, 1994; Rogers & Harpending, 1992; Rogers, 1995; Rogers & Jorde, 1995; Sherry *et al.*, 1994; Slatkin & Hudson, 1991). The method involves analysis of nucleotide sequence differences between pairs of individuals (mismatches) within a population and the frequency distribution of pairwise differences. If a population has been of relatively constant size for a very long time, then its mismatch distribution tends to be multimodal or ragged (Harpending *et al.*, 1993). If a population has passed through a bottleneck or expanded from a small initial size, then its distribution tends to be unimodal. In this case, the mode of the distribution is often approximately proportional to the time since expansion. The number of mutations within a population increases through time, so the mode, mean and maximum number of pairwise differences increases (Figure 1). If

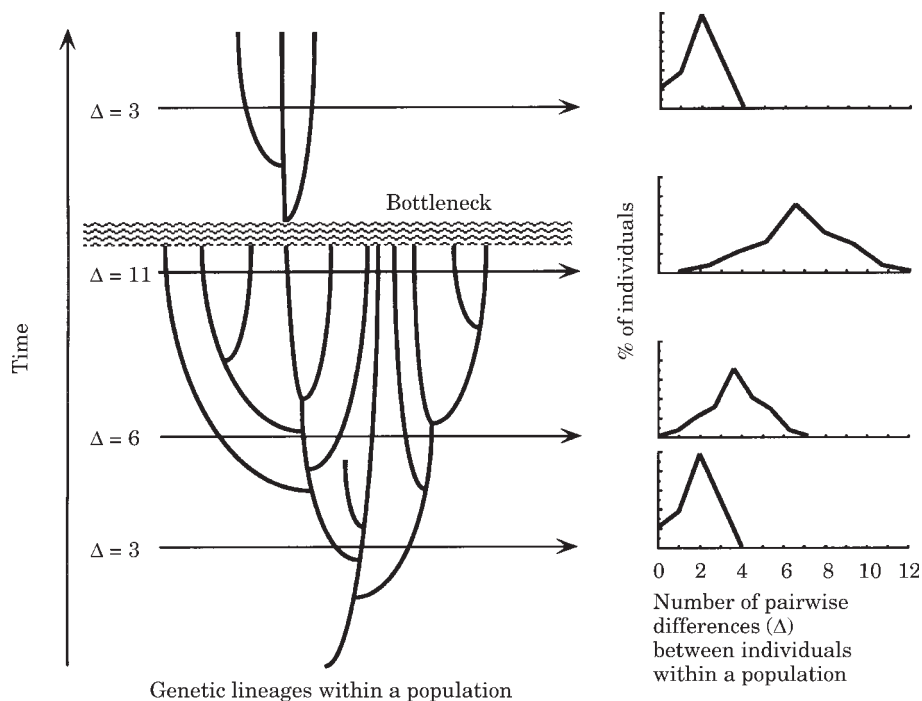


Figure 1. An idealized illustration of mismatch distributions within a population through time. The number of mismatches or pair-wise differences (Δ) between individuals within a population increases through time due to the accumulation of mutations. The frequency distribution of pair-wise differences is strongly unimodal in populations that have been reduced to a size small enough to eliminate most genetic diversity. The mode, mean and maximum pairwise difference increases as mutations accumulate through time.

mutation rates are known, then the time since release can be estimated, but an assumption must be made about population size through the bottleneck (Relethford & Harpending, 1995). Larger populations contain more alleles; therefore higher diversity could be interpreted as an earlier release.

How small was the bottleneck? Jones & Rouhani (1986) suggest it could reflect a total Old World breeding population of 40 individuals for two centuries or 4000 individuals for 20,000 years. Harpending *et al.* (1993) provided estimates as low as 500–3000 females. Rogers & Harpending (1992) suggested less than 2000 breeding females and Rogers & Jorde (1995) suggests no less than 1000. Haigh & Maynard Smith (1972) calculated an effective population size of less than 10,000. Ayala & Escalante (1996;

Ayala, 1995, 1996b) suggest population size never fell below 4300 individuals. The highest estimates of effective population size are about 10,000 reproductive females (Takahata *et al.*, 1995; Klein *et al.*, 1993; Erlich *et al.*, 1996; Sherry *et al.*, 1997). Population size was never significantly lower than this for an extended period (Takahata, 1993). Although an effective population size of 10,000 is not considered a bottleneck by some of these authors, it is very small if divided among small demes (Rogers & Jorde, 1995).

Some researchers have suggested a bottleneck did not occur, based on analyses of genes in the Major Histocompatibility Complex (Klein *et al.*, 1993). MHC polymorphisms, including the Human Leukocyte Antigen complex (Ayala, 1995;

Ayala & Escalante, 1996) are, however, under strong positive selection because of their fundamental role in antigenicity and disease resistance. They are problematic for reconstructing evolutionary and population history (Erlich *et al.*, 1996; Hickson & Cann, 1997).

Bottlenecks in other species. The genetic structure of eastern African chimpanzee populations (*Pan troglodytes schweinfurthii*) (Morin *et al.*, 1994) suggests they survived one or more bottlenecks in the Late Pleistocene (Rogers & Jorde, 1995; Goldberg, 1996). Several populations that reside within the Pleistocene ice age eastern forest refugium of the montane region centered on western Uganda and eastern Zaïre (Hamilton, 1976), have mismatch distributions that suggest they experienced a release from a bottleneck ~67 ka. This date closely coincides with the start of the last ice age (oxygen isotope stage 4, 70–74 ka). Populations outside of the core Pleistocene refugium seem to have been released from a bottleneck much more recently, possibly after the Last Glacial Maximum (LGM, oxygen isotope stage 2), around 20 ka (Goldberg, 1996). The later release may also be evinced by a bimodal distribution of pairwise differences in mitochondrial DNA sequences in the core refugium populations. The modes are centered on ~67 and ~20 ka (Goldberg, 1996). Bimodal mismatch distributions can be interpreted in other ways (Marjoram & Donnelly, 1994), but the fit of these chimpanzee data with known environmental history suggests the hypothesis that some populations experienced two bottlenecks and releases during or after the two coldest parts of the last glacial.

Mismatch analysis of population structures and histories have been determined for few other species. Cheetahs apparently experienced two severe population bottlenecks in the very recent past (O'Brien *et al.*,

1987). The earlier one, estimated to have occurred ~10 ka, may reflect dramatic reduction in the extent of savanna grassland environments at the beginning of the early Holocene wet phase (isotope stage 1, ~12 ka). Because cheetahs are adapted to open, arid environments, they are unlikely to be affected by environmental change involving reduction of forests. Their population history is thus expected to be out of phase with that of chimpanzees. I am not aware of research identifying bottlenecks in other large mammals species. Reconstructing population history with mismatch analysis requires a long, labor-intensive process of generating sequence data on many individuals within a population. Goldberg's (1996) monumental pioneering research on chimpanzees should be emulated with analysis of the genetic structure of other species adapted to humid tropical environments.

The Weak Garden of Eden. The Weak GOE model (Harpending *et al.*, 1993; Sherry *et al.*, 1994) is a variant of the Replacement model that incorporates bottlenecks and releases during the Upper Pleistocene (Figure 2). The model posits a dispersal of African modern humans from a restricted source into separate regions around 100 ka, but without significant population expansion. This was followed by bottlenecks in the dispersed, subdivided populations. The cause of bottlenecks is not explained in the Weak GOE. "Later, starting around 50,000 years ago, dramatic population growth and expansion occurred separately within dispersed daughter populations that were genetically isolated from each other" (Harpending *et al.*, 1993: 495). Population growth after the bottleneck is thought to have been initiated by the invention of a more efficient Later Stone Age/Upper Paleolithic (LSA/UP) technology in Africa, which increased environmental carrying capacity (Harpending *et al.*, 1993; Sherry *et al.*, 1994).

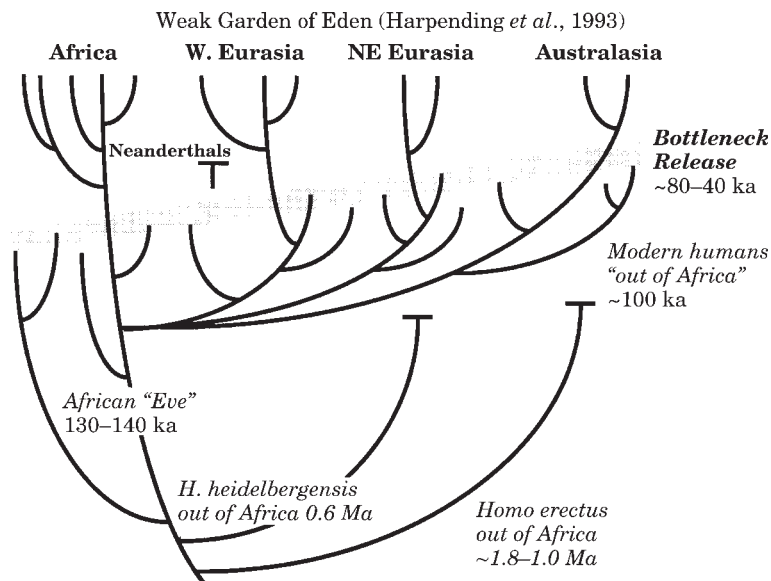


Figure 2. The Weak Garden of Eden model of Harpending *et al.* (1993; Sherry *et al.*, 1994). Anatomically modern humans evolved from a small population in the late Middle Pleistocene, dispersed from the area of origin, subdivided, and replaced archaic populations in the early Upper Pleistocene. Each population passed through a bottleneck after subdivision and/or dispersal. Later, they expand in number following the invention and diffusion of modern (Later Stone Age and Upper Paleolithic) technology.

In this scenario of population history the geographic locations or sizes of the dispersed, genetically isolated daughter populations are not clearly specified. This model implies initial dispersal and differentiation of modern human populations occurred within Africa, but after bottlenecks, the later expansions of genetically isolated populations are illustrated as having occurred earliest in Africa and latest in Eurasia (Harpending *et al.*, 1993, 1996; Sherry *et al.*, 1994), implying population subdivision and dispersal to other continents may have occurred before bottlenecks. If population growth is related to the invention and spread of advanced technology from a single source region then it seems to imply that at least some modern human populations had already dispersed from Africa to Eurasia before they adopted the new innovations. The Weak GOE model does not posit a replacement of local archaic populations by modern ones at the time of population

expansion (perhaps with the exception of the neanderthals), rather, it suggests replacement of earlier Middle Paleolithic by Upper Paleolithic technologies among populations after their dispersal. If the Weak GOE scenario is correct, and if release from a bottleneck occurred earliest in subsaharan Africa, then the earliest examples of modern human technology and modern behavior should be found there. Archaeological evidence suggests, but does not conclusively demonstrate, that the Middle Stone Age (MSA) to Later Stone Age transition occurred around 50 ka in East Africa, and thus earlier than the Middle Paleolithic (MP) to Upper Paleolithic transition in west Asia (Ambrose, 1998).

Replacement with bottlenecks and Multiple Dispersals. The most detailed and cogent model of the origin and spread of modern humans has been proposed by Lahr & Foley (1996; Lahr & Foley, 1994; Foley & Lahr,

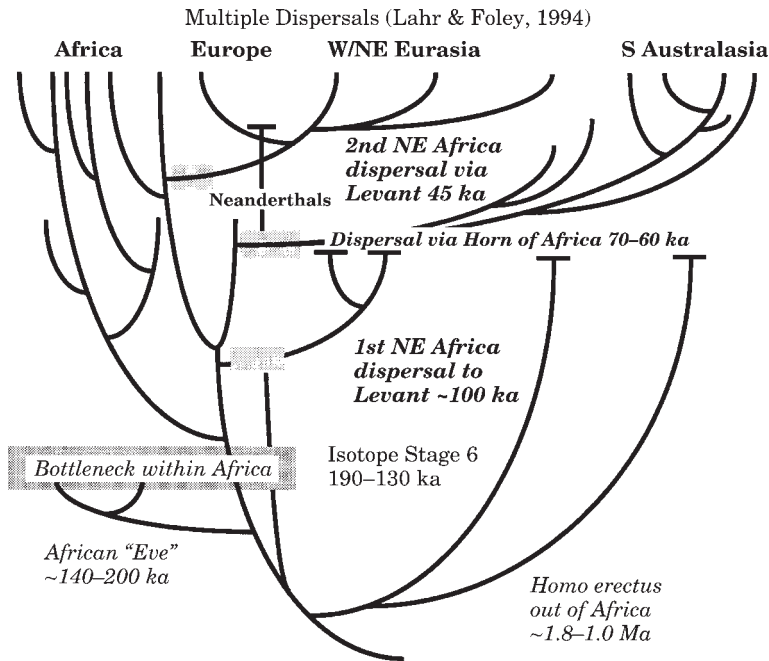


Figure 3. The Multiple Dispersals model of Lahr & Foley (1994; Lahr, 1996). Modern human populations experienced bottlenecks within Africa during the penultimate glacial (oxygen isotope stage 6, 190–130 ka) and at points of dispersal across narrow land bridges and seaways. The first dispersal, to southwest Asia around 100 ka, did not result in permanent replacement of Neanderthals. The second dispersal, to tropical Australasia across the Bab el Mandeb Straits during the first half of the last glacial, and third dispersal, across the Sinai to the Levant around 45 ka, resulted in permanent replacement of archaic hominids outside Africa.

1997). The Multiple Dispersals model (Figure 3) proposes that a population bottleneck occurred during oxygen isotope stage 6, when cold, dry climates caused isolation and differentiation of populations within Africa. Additional bottlenecks, followed by population expansions, could have occurred during dispersals from Africa through physical bottlenecks such as the Sinai Peninsula and the Bab el Mandeb Straits. The first dispersal of anatomically modern humans followed the northeast route out of Africa across the Sinai Peninsula to the Levant ~100 ka, during warm, humid oxygen isotope stage 5. Early modern human skeletons at the Levantine cave sites of Skhul and Qafzeh and their associated Afro-Arabian biota provide the hard evidence for this dispersal event

(Stringer & Andrews, 1988; Tchernov, 1992a, 1992b; Bar-Yosef, 1994). At the beginning of the last ice age the Afro-Arabian biotic community of the southern Levant was abruptly replaced by a Palearctic one, including cold-adapted neanderthals (Tchernov, 1992a, 1992b; Bar-Yosef, 1994). Southwest Asia is considered a cul-de-sac in the multiple dispersals model (Lahr, 1996), so these early modern Africans failed to reach points farther east or north. Equipped with an MP technology similar to that of the neanderthals, early modern humans apparently lacked technological competitive superiority, and were either eliminated or pushed south into Africa and/or to the southern Arabian Peninsula at the start of the last glacial. The failure of early modern humans to survive in

the Levant during the early last glacial implies they were not yet physiologically and/or behaviorally well-adapted to cold climates and Palearctic environments, or at least not as well-adapted as neanderthals. The first dispersal thus apparently failed to permanently establish modern humans outside of Africa.

Genetic evidence shows non-African populations can be divided into southern Australasian and northern Eurasian populations (Cavalli-Sforza *et al.*, 1988, 1994; Nei & Roychoudhury, 1993). Further analysis suggests these macro-regional populations divided 50–75 ka (Mountain & Cavalli-Sforza, 1997). To explain this deep and early division, Lahr (1996; Lahr & Foley, 1994) proposed the African ancestors of modern tropical Australasian populations successfully dispersed from Africa via a southern route before they successfully dispersed to western and northern Eurasia. Following Kingdon (1993), they posit an Indian Ocean coastal dispersal route to tropical Australasia, from the Horn of Africa via the southern Arabian Peninsula, across the Bab el Mandeb Straits at the southern end of the Red Sea. Crossing the Red Sea would have been facilitated by low sea levels during the last glacial period, presumably during oxygen isotope stage 4 (74–60 ka), or early stage 3 (60–45 ka). Fossil and archaeological evidence for this dispersal is scarce, and largely relies on evidence for the occupation of Australia by 40–60 ka (Lahr & Foley, 1994).

The final dispersal event, at around 45 ka, was again via the northeast corner of Africa, via the Sinai Peninsula to the Levant. This coincided with the transition from the Middle to the Upper Paleolithic in western Asia, Europe and southern Siberia. This dispersal, by anatomically modern African humans bearing behaviorally modern human technology, led to replacement of neanderthals and other archaic human populations in Europe and higher latitudes

of western Asia. The European and west Asian fossil and archaeological records seems consistent with a late dispersal and replacement (Klein, 1989a; 1992, 1995). Refined radiocarbon chronologies (Ambrose, 1997, 1998) suggest the transition from the MSA to the LSA occurred ~50 ka in East Africa; the MP to the UP occurred ~47–43 ka in the Levant (Bar-Yosef *et al.*, 1996) and 43–40 ka in western Europe and Siberia (Bischoff *et al.*, 1994; Mercier *et al.*, 1995; Goebel & Aksenov, 1995; Goebel *et al.*, 1993).

The Multiple Dispersals model cogently integrates the available genetic, fossil and archaeological evidence with that from paleobiogeography and paleoclimatology. The explanation for the bottleneck proposed below may be more consistent with the Weak GOE model but does not necessarily invalidate the Multiple Dispersals scenario unless it critically depends on the timing of bottlenecks. A scenario of globally synchronous bottlenecks is considered below.

What caused Late Pleistocene bottlenecks?

Geneticists have not offered explanations for bottlenecks in dispersed Late Pleistocene populations and few outside their field have paid much attention to this remarkable event in human population history. Paleoanthropologists, except for Lahr (1996; Lahr & Foley, 1994) have generally not acknowledged its existence and implications, nor offered explanations for its cause. The hypothesis proposed below (also see Rampino & Ambrose, *in press*) makes a bottleneck seem inevitable. The causes of bottlenecks and releases are separate issues because these events may have been widely separated in time and may have resulted from entirely different processes that need to be considered separately. This unusual series of events raises several fundamental questions:

- (1) What caused the bottlenecks? Could it have been epidemic diseases, global climate change, dispersal of small founding populations through physical geographic bottlenecks, or a global catastrophe analogous to the cometary impact at the Cretaceous-Tertiary boundary?
- (2) When did bottlenecks occur? Did different populations experience bottlenecks at different times? Did populations experience more than one bottleneck?
- (3) How long did bottlenecks last, and when did populations expand? Were releases soon after bottlenecks occurred, or were populations small for a very long time? Were releases synchronous in different populations, or did they occur earlier in some populations and later in others? Was there more than one release in a population?
- (4) What caused population expansion? Was it the growth of disease-resistant populations, exponential growth of founding populations in new environments, global climate change or the spread of technological innovations?
- (5) Where were releases first initiated: sequentially from Africa to the peripheries of the Old World, simultaneously everywhere, or wherever founding populations were established?

Cause and timing of bottlenecks

Epidemic disease. Were global populations decimated by epidemic diseases? Extremely contagious diseases and/or high population densities would be required to sustain transmission. Epidemics could only be recognized in the fossil record by skeletal pathologies or catastrophic mortality profiles of large skeletal populations. This hypothesis is currently untestable.

Founder effects. The founder effect in a small dispersing population crossing barriers to

gene flow, such as the Sinai desert or the Bab el Mandeb Straits, could undoubtedly appear as asynchronous bottlenecks in the genetic structure of populations in different regions. This explanation is plausible in Lahr's (1996; Lahr & Foley, 1994) Multiple Dispersals scenario.

Global climate change. Global climate change could have reduced populations during the early last ice age, oxygen isotope stage 4 (74–60 ka) or during stage 6 (190–130 ka). It is notable that the southern Levantine fossil record shows the abrupt replacement of the Afro-Arabian by the Palearctic biotic community at the stage 5/4 boundary (Tchernov, 1992a, 1992b). The high resolution pollen record from Grand Pile, France (Woillard, 1978; Woillard & Mook, 1982), shows the rapid onset of cold, dry steppe conditions at ~70 ka. Low primary productivity during the last ice age could have significantly reduced human population size. As noted above, the replacement of modern humans by neanderthals in the Levant, suggests African modern humans were rather poorly-adapted to cold climates.

Volcanic winter. Was a cataclysmic geological event responsible for the bottleneck? Rampino & Self (1992, 1993; Rampino *et al.*, 1988) have proposed that the super-eruption of Mt Toba, located in northwest Sumatra, caused a volcanic winter lasting several years. The Toba eruption is dated to $\sim 73,500 \pm 2000$ bp by K/Ar (Chesner *et al.*, 1991) and in ice cores it is dated to 71 ka (Zeilinski *et al.*, 1996a, 1996b). Toba was an order of magnitude larger than any other known Quaternary explosive volcanic eruption (Dawson, 1992; Rose & Chesner, 1990; Huff *et al.*, 1992) and is widely considered to have had a significant impact on Quaternary climate, possibly contributing to the rapid onset and extreme cold of stage 4 (Rampino & Self, 1992, 1993).

Toba's volcanic ash can be traced west across the Indian Ocean and northwest across India (Rose & Chesner, 1990). In some Indian Ocean cores the ash is over 12 cm thick (Dawson, 1992). It is a widespread terrestrial marker bed in India, where it occurs as primary and reworked airfall ash, in beds that are commonly one to three, and occasionally up to six meters thick (Acharyya & Basu, 1993).

The dense rock equivalent (DRE) volume of a volcanic ash layer is a standard measure of the magnitude of an explosive eruption. The largest known eruption of the last 454 million years is represented by the Ordovician Millbrig Beds in eastern North America, which correlate with the Big Bentonite of northwestern Europe (Huff *et al.*, 1992). The Millbrig/Big Bentonite DRE is 1140 km³ of solid rock (Huff *et al.*, 1992). Tambora F5, the largest known historic eruption, displaced 20 km³ and Mt St Helens produced 0.2 km³ of volcanic ash (Huff *et al.*, 1992). Toba had a DRE of about 800 km³ (Rose & Chesner, 1990). It was thus 40 times larger than the largest eruption of the last two centuries and apparently the second largest known explosive eruption in Phanerozoic history.

The high-resolution record of climate and explosive volcanism in Greenland ice cores clarifies the chronostratigraphic position of the Toba super-eruption, its relationship to the onset of the last ice age and to dramatic climatic deterioration at 71 ka (Zielinski *et al.*, 1996a, 1996b; Dansgaard *et al.*, 1993). Oxygen isotope ratios, calcium and sulfur concentrations and electrical conductivity of ice show Toba erupted about 71 ka, between the interstadials (warm periods) of Dansgaard-Oeschger (D-O) events 19 and 20 (Zielinski *et al.* 1996b). The eruption is marked by a 6-year period during which the largest amount of volcanic sulfur of the last 110 ka was deposited in the ice core, and marks the termination of the interstadial of D-O event 20. This dramatic volcanic event

is followed by 1000 years of the absolutely lowest ice core oxygen isotope ratios of the last glacial period. In other words, for 1000 years immediately following the Toba eruption, the earth witnessed temperatures relentlessly colder than during the Last Glacial Maximum at 18–21 ka. The first 200 years of this stadial event are marked by increased calcium deposition, indicating high atmospheric dust concentrations, probably from aeolian erosion due to reduced vegetation cover and sediments exposed by a drop in sea level.

The interstadial portion of D-O event 19, which was a warm period that lasted for approximately 2000 years following this coldest millennium, shows that Toba was not directly responsible for the onset of the last glacial, which occurs in the ice core ~68 ka (Zielinski *et al.*, 1996b). The discrepancy in dating of the eruption of Toba and onset of the last ice age (stage 4) between K/ar (Chesner *et al.*, 1991), deep sea (Martinson *et al.*, 1987) and Greenland ice records (Zielinski *et al.*, 1996b; Dansgaard *et al.*, 1993) may reflect differences in methods of estimating ages. The ice core dates are estimated by ice deposition rates in ice older than 50 ka, rather than counting of annual layers.

The global climatic impact of explosive volcanic eruptions is controlled by several factors (Handler, 1989; Sigurdsson, 1990; Rampino & Self, 1988). First, the eruptive plume must reach a height greater than 17 km, into the stratosphere, before volcanic aerosols can be effectively globally redistributed. Several historic eruptions that have altered global climate had plume heights far greater than 17 km (Sigurdsson & Carey, 1988). Toba's plume probably reached twice this height (Rampino & Self, 1992). Most solar energy falls at low latitudes, so eruptions near the equator cause much more substantial cooling due to the reflection of solar energy. The reduction in atmospheric visibility due to volcanic ash and dust

particles is relatively short-lived, however, on the order of three to six months (Sigurdsson, 1990). Longer-term global climatic cooling is caused by the high reflectance of sulfuric acid haze (Handler, 1989). Sulfuric acid molecules stay suspended in the upper atmosphere for several years.

Ice core evidence provides the "smoking gun" that implicates Toba as cause of the coldest millennium of the late Pleistocene. It shows Toba injected more sulfur that resided in the atmosphere for a longer time (6 years) than any other volcanic eruption in the last 110 ka (Zielinski *et al.*, 1996a, 1996b). These ice core geochemical data confirm the original estimates (Rampino *et al.*, 1988; Rampino & Self, 1992; Sigurdsson, 1990) for the volcanic winter scenario.

If volcanic winter also led to rapid expansion of snow cover, it would have altered albedo and perpetuated longer-term cooling. Ice core oxygen isotope data show the coldest millennium of the Upper Pleistocene followed Toba's volcanic winter (Zielinski *et al.*, 1996a, 1996b). Other climatic records may also reflect Toba's impact. In the Grand Pile pollen record, the Stadial 1 (isotope stage 4) environment is described as "particularly rough", an adjective used nowhere else in the description of a record spanning 140 ka (Woillard, 1978). Long pollen sequences from the Bandung area of Java and marine sediments in Indonesia (van der Kaars, 1991; van der Kaars & Dam, 1995, 1997) and paleobiogeographic evidence indicate large parts of southeast Asia were deforested at this time (Brandon-Jones, 1996; Flenley, 1996).

The climatic effects of volcanic eruptions can have severe consequences for human populations (Rampino *et al.*, 1988; Handler & Andsager, 1994; Sigurdsson, 1990). The effects of Toba's volcanic winter on terrestrial plant productivity are described in greater detail elsewhere (Rampino *et al.*,

1988; Rampino & Ambrose, *in press*). Tambora caused the year without a summer in 1816 (Harrington, 1992), with snow in July and August in New England and global crop failures and famines (Sigurdsson & Carey, 1988; Ramaswamy, 1992). The Toba super-eruption is estimated by Rampino & Self (1993) to have lowered sea surface temperatures by 3–3.5°C for several years. At higher latitudes the cooling effect would have been substantially amplified. Rampino & Self (1993) estimate a 12°C reduction in summer temperatures at the latitude of Quebec for two to three years following the super-eruption, and longer term cooling due to increased reflectance of solar energy (reduced albedo) caused by greater snow cover. If Tambora caused the year without a summer in 1816, Toba could have been responsible for six years of relentless volcanic winter, substantial lowering of plant biomass and disastrous famine (Rampino *et al.*, 1988; Rampino & Self, 1992, 1993; Rampino & Ambrose, *in press*).

Deep sea cores have probably failed to resolve the magnitude of this event and its impact on terrestrial environments because chronological resolution is usually limited to millennial scale events due to low deposition rates, sediment bioturbation, secondary transportation of microfossils and thickness of sampling intervals (Schindel, 1982; Schiffelbein, 1984; Martin, 1993; Kidwell & Flessa, 1995; Roy *et al.*, 1996). Differences in power to resolve short-term climate events are well illustrated by comparisons of Greenland ice core with North Atlantic microfossil and isotopic records (Bond *et al.*, 1993; Jouzel, 1994). Only one study of deep sea cores has achieved sub-millennium-to century-scale resolution of climate change by closely-spaced sampling intervals (Bond *et al.*, 1997).

Isolating this millennium in the archaeological record seems highly improbable given the difficulties of precisely and accurately dating occurrences in this time range.

Perhaps rock shelters in the path of the Toba ash plume, northwest of Sumatra (southern India and the Arabian Peninsula) preserve a layer of ash from this eruption that could be used as an isochron. Determining the effect of volcanic winter on human morphology would be even more difficult because of the scarcity of well-dated human fossils. The possible effects of large volcanic eruptions on mammalian morphology has only been well-documented in a Miocene sequence in Argentina that contains large samples of fossils from a continuous sedimentary sequence (Anderson *et al.*, 1995).

Paleobiologists have traditionally focused on understanding the effects of long term climate changes and climatic regimes (glacial-interglacial cycles) on biogeography, population history, adaptation and evolution (Potts, 1996; Boaz, 1997). However, short-term, high amplitude climatic variations on decadal to sub-millennial scales may have had substantial and immediate impacts on species distributions (Roy *et al.*, 1996) and population histories. It would be valuable to follow the lead of Zielinski *et al.* (1996a, 1996b), who have the luxury of studying an ice core record that provides annual resolution. Intensive micro-sampling of stratigraphic sections in deep sea cores, lakes, bogs and varved fluvial sequences for isotopic, geochemical, botanical, faunal and sedimentological analyses (Burnham, 1993; Webb, 1993; Bond *et al.*, 1997), and isotopic analysis of incremental structures in speleothems, tree rings and corals (Schwarcz, 1986; Yapp & Epstein, 1982; Beck *et al.*, 1997) that span the stage 5/4 boundary, should be performed in order to further assess Toba's impact on global climate and low-latitude environments.

Famine caused by the Toba super-eruption and volcanic winter provides a plausible hypothesis for Late Pleistocene human population bottlenecks. Six years of volcanic winter, followed by 1000 years of the coldest, driest climate of the Late

Quaternary, may have caused low primary productivity and famine, and thus may have had a substantial impact on human populations (Rampino & Ambrose, *in press*). Many local human populations at higher latitudes and in the path of the ash fallout may have been eliminated. This may explain the extraordinary magnitude of the bottleneck effect recorded in our genes. Figure 4 illustrates a revised Weak Garden of Eden model that incorporates both the effect of volcanic winter and the Multiple dispersals scenario of Lahr & Foley (1994).

Neanderthals had a more cold-tolerant anatomy (Trinkaus, 1981, 1989; Holliday, 1997), and may have been less affected by this event. The effects of volcanic winter on them may never be known if they left no modern descendants. However, ancient neanderthal DNA has now been recovered (Krings *et al.*, 1997). If DNA can be extracted from a large number of neanderthals their population genetic structure could be examined for bottlenecks by mismatch analysis.

The cause, timing and location of bottleneck releases

If population release was due to the natural increase (logistic population growth) of disease-resistant populations following epidemics, then growth could have been relatively rapid, a function of the intrinsic rate of increase of disease-resistant populations, and the duration of the bottleneck relatively brief. Its date could have been at any time, but would presumably have been relatively soon after the bottleneck. Release could have occurred wherever disease-resistant individuals survived.

If release was due to natural increase in founder population size after dispersing across land bridges or narrow straits (Lahr, 1996; Lahr & Foley, 1994) then release dates would vary from ~70–50 ka for the early Australasian dispersal, to ~45 ka for the second Levantine dispersal. In the

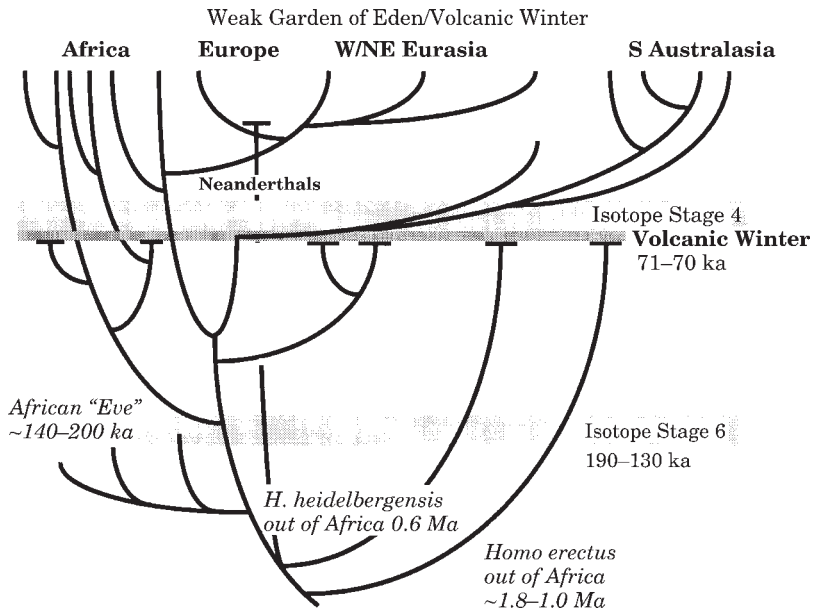


Figure 4. The Volcanic Winter/Weak Garden of Eden model proposed in this paper. Population subdivision due to dispersal within African and to other continents during the early Late Pleistocene is followed by bottlenecks caused by volcanic winter, resulting from the eruption of Toba, 71 ka. The bottleneck may have lasted either 1000 years, during the hyper-cold stadial period between Dansgaard-Oeschger events 19 and 20, or 10 ka, during oxygen isotope stage 4. Population bottlenecks and releases are both synchronous. More individuals survived in Africa because tropical refugia were largest there, resulting in greater genetic diversity in Africa.

epidemic and dispersal scenarios the duration of the bottleneck would have been brief.

If a bottleneck occurred during stage 6 (Lahr & Foley, 1994), the release would date to the onset of warm climate at the beginning of stage 5, ~130 ka. This date is not significantly different from the date of the origin of modern humans estimated from the coalescence of mtDNA sequences to "Eve" by Stoneking *et al.* (1992). The species origin is by definition a bottleneck because only one mtDNA sequence survives from that time, though others undoubtedly existed. However, the bottlenecks identified by Harpending *et al.* (1993) that require explanation occurred long after Eve.

If bottlenecks were caused by the cold, arid climate of isotope stage 4 then their duration was approximately 10 ka and release could have been as late as 60 ka. If Toba alone caused the bottleneck, then

release could have been within a few decades of volcanic winter at ~71 ka. If the bottleneck persisted for the entire coldest millennium following the eruption, then release would have coincided with D-O event interstadial 19, around 70 ka. In these climate-induced bottleneck scenarios the surviving populations would have expanded simultaneously when favorable climates returned.

Harpending *et al.* (1993) proposed that the release was due to the invention of a more effective UP or LSA technology in subsaharan Africa. Improved technology would have increased the effectiveness of human adaptations, including access to a larger, more reliable food supply, and would have led to an increase in population size. The earliest LSA industry in Africa appears ~50 ka at the site of Enkapune Ya Muto rockshelter in the central Rift Valley of

Kenya (Ambrose, 1997; Ambrose, 1998). Three sites in Tanzania (Mumba Höle, Nasera and Naisiusu at Olduvai Gorge) may have a similar antiquity (Mehlman, 1989, 1991; Brooks & Robertshaw 1990; Manega, 1993). The MP/UP transition dates to around 47 ka in the Levant and about 43 ka in Europe and Siberia (Ambrose, 1997; Bar-Yosef *et al.*, 1996; Marks, 1983; Mercier *et al.*, 1995; Bischoff *et al.*, 1994; Goebel & Aksenov, 1995; Goebel *et al.*, 1993; Koslowski, 1988). The chronology of the transition from archaic to modern human technology thus fits the genetic evidence for a wave of advance mode of time-transgressive releases from the bottleneck in different regional populations (Harpending *et al.*, 1993; Sherry *et al.*, 1994). In other words, release earliest in subsaharan African, and latest European and Asian populations in response to improved technologically-mediated adaptations.

Is there a clear relationship between the release from the bottleneck and the origin of modern technology? If the bottleneck occurred ~70–60 ka, this does not necessarily mean that it caused technological and behavioral changes that occurred 10–20 ka later. However, Africa apparently had the largest surviving population through the bottleneck (Relethford & Harpending, 1994), probably because of the large size of its tropical refugia. By analogy with a larger reservoir of genetic diversity, one could hypothesize that Africans may have maintained the largest reservoir of accumulated knowledge on which to base new technological and social innovations that characterize the LSA and UP.

Pleistocene population size and distribution

African archaeological evidence

Does the archaeological record support the hypothesis that a Pleistocene population

explosion accompanied transition to modern technology (Harpending *et al.*, 1993; Sherry *et al.*, 1994)? The archaeological record of the early last glacial period in southern and northern Africa seems to show very low population densities throughout most of the last ice age. In arid regions of Africa, MSA/MP and early LSA/UP occurrences dating to isotope stages 3 and 4 (24–74 ka) are remarkably scarce in comparison to those of the last interglacial (stage 5) and the Holocene (stage 1). Caves and rockshelter sites that preserve sediments dating to both the last interglacial and last glacial have relatively abundant traces of occupation during oxygen isotope stage 5, while last glacial layers have very low densities of cultural materials (Butzer, 1988; Klein, 1989b; Deacon, 1995). Sedimentation with sparse intervals of human occupation occurs in several rockshelters during the last glacial, for example, at Border Cave (Beaumont *et al.*, 1978), Boomplaas (Deacon *et al.*, 1984) and Die Kelders (Grine *et al.*, 1991) in South Africa, suggesting the paucity of human occupation evidence is not an artifact of erosion or sampling bias.

Most MP sites in the Sahara and North Africa appear to date to the last interglacial (Wendorf & Schild, 1992). Only one early UP site is known to date to between 40 and 30 ka in the Nile Valley (Vermeersch *et al.*, 1984). Sodmein Cave, in the Red Sea Mountains of Egypt, also has sparse last glacial MP and early UP horizons (Van Peer *et al.*, 1996). The Haua Fteah, a huge cave on the coast of Libya, contains a continuous sedimentary record through the last glacial, but with very low densities of MP artefacts (McBurney, 1967). Culturally sterile sediments accumulated between last interglacial and glacial and between MP and early UP occupations. The earliest UP, which dates to almost 40 ka, is only known from Haua Fteah and Hagfet et Dabba caves (McBurney, 1967). In the Kenya Rift

Valley, the dating of the late MSA remains uncertain and industries transitional to the LSA are unknown. The early LSA is known only from Enkapune Ya Muto, where it apparently began ~50 ka (Ambrose, 1998).

Rockshelters in northern Tanzania seem to have more continuous occupation through the Upper Pleistocene and transitional MSA/LSA industries seem to occur around 30–50 ka (Mehlman, 1989, 1991; Brooks & Robertshaw, 1990). Continuous sequences of archaeological cultures from the late Middle Pleistocene to the early Holocene can also be inferred for the Sangoan to Lupemban to Tshitolian industries in equatorial central Africa (Van Noten, 1982) and Sangoan to Charaman to Bambatan to Tshangulan/Maleme industries in Zimbabwe and southern Zambia (Clark, 1982: 318; Brooks & Roberstshaw, 1990; Walker, 1995).

Archaeological evidence thus suggests African hunter-gatherers fared poorly in cold, arid environments at higher latitudes during the early last ice age, and seem to have abandoned these regions or lived at population densities below the threshold of archaeological visibility (Butzer, 1988). Continuity of lithic technologies within the MSA or from the MSA to the LSA and MP to the UP cannot be demonstrated in more arid parts of southern, northern or eastern Africa. Humans apparently survived without significant discontinuities in material cultural traditions in warmer, wetter equatorial regions, suggesting this region may have been a large population reservoir during the last glacial and volcanic winter. However, there is no evidence for an increase in the number of archaeological sites during the MSA/LSA or MP/UP transitions in Africa. Therefore the African archaeological record does not support the hypothesis (Harpending *et al.* 1993; Sherry *et al.*, 1994) that a Pleistocene population explosion accompanied transition to modern technology. However, few sites of this time range

have been excavated and they are difficult to date accurately (Ambrose, 1997; Ambrose, 1998), so the limited evidence does not actually refute this hypothesis. Improved dating techniques (Renne *et al.*, 1997) that can be applied in regions of active volcanism like East Africa may be useful for further evaluating this hypothesis.

Pleistocene population refugia

Tropical areas of high rainfall may have served as biotic population refugia during volcanic winter and isotope stage 4. Several refugia have been identified in Southeast Asia (Brandon-Jones, 1996), including Java, northeastern Indochina (including southern China) and southern India. Southern India should have been a relatively large tropical refugium, but it was effectively buried by ash from Toba (Acharyya & Basu, 1993). Only the southern tip of the Indian subcontinent (the western Ghats) seems to have served as a refugium for tropical primates during the last glacial (Brandon-Jones, 1996). At present sea level the available land area in southeast Asia is small and fragmented into islands and peninsulas. Although substantially larger land areas east, north and south of Toba were exposed during times of low sea level (the Sunda and Sahul shelves), they would only have been exposed after the Toba super-eruption and onset of isotope stage 4. Reconstructions of paleobiogeography and paleoclimatology of tropical southeast Asia during the last and penultimate glaciations suggest deforestation and cold dry climates (van der Kaars & Dam, 1995; Brandon-Jones, 1996). It thus seems unlikely that large human populations could have survived volcanic winter in tropical Australasia.

The continent with the largest land area over the equator would have maintained the largest population through the bottleneck. Africa has the largest well-watered land area over the equator. Three major refuge areas in equatorial Africa have been identified

(Hamilton, 1976), located in far West Africa, west-central Africa, and the montane eastern margin of the Congo basin. In each refugium annual rainfall is currently greater than 2000 mm. Additional refugia may have been located along the south coast of South Africa in the vicinity of the Knysna forest, highland Ethiopia, the Nile Valley and the Atlas mountains of NW Africa. Archaeological evidence discussed above suggests the largest human populations during the bottleneck probably survived in equatorial Africa. Indeed, genetic evidence suggests some equatorial African populations experienced population growth around 110 ka, and did not experience a significant bottleneck at the beginning of the last glacial (Watson *et al.*, 1997).

Population age vs. size through the bottleneck: implications for genetic diversity

Does Africa necessarily have the oldest modern human genome? Africans have the greatest genetic diversity by most measures (but see Jorde *et al.*, 1995; 1997; Relethford, 1997) and this diversity is widely assumed to be a function of the greater age of African populations (Cann *et al.*, 1987; Harpending *et al.*, 1993). Genetic diversity is, however, also a function of population size. Relethford & Harpending (1994, 1995; Relethford, 1995, 1997) note that diversity due to large population size can be incorrectly interpreted as being due to greater population age. This poses problems for the phylogenetic interpretation of the African ancestry of modern humans (Relethford & Harpending, 1995; Relethford, 1995). Africa has the largest tropical land area over the equator and would have been the largest refugium for humans during volcanic winter. Africans may have passed through a bottleneck with the greatest genetic diversity simply because of population size. Relethford & Harpending (1994) estimate African population size through the bottleneck was three times larger than elsewhere.

Large population size may have also permitted an earlier bottleneck release and a larger reservoir of behavioral variation and capacity for innovation.

Human population history during the Later Pleistocene

The pattern of human population changes proposed by Haigh & Maynard Smith (1972) is illustrated in Figure 5(a). Modifications to account for late Quaternary environmental and cultural changes are shown in Figure 5(b). If the bottleneck was caused by the cold millennium following volcanic winter and/or the severe climate of oxygen isotope stage 4, then the duration of the human bottleneck and date of its release are likely to have been either 1000 years and 70,000 bp, or 10,000 years and 60,000 bp. If mutation rates can be accurately determined, it should be possible to use the genetic structure of modern human populations to make relatively precise estimates of population sizes through the bottleneck in different regions.

Mismatch data suggest Pleistocene populations were largest in Africa and smallest in Australasia (Relethford & Harpending, 1994, 1995). It is unclear if this revision of the Weak GOE invalidates the hypothesis of earlier releases from bottlenecks in Africa due to improved technology (Harpending *et al.*, 1993; Sherry *et al.*, 1994). Climatic and technological releases from a bottleneck are unlikely to have occurred at the same time, but both may have played a role in Late Pleistocene population growth after volcanic winter and the onset of the last ice age. Climatic release may have occurred first, around either 70 or 60 ka, with technologically-aided release trailing at ~50 ka, beginning in Africa and spreading to Eurasia by ~45–40 ka, as modern humans and/or modern LSA/UP technology diffused from the African source area. Is it possible to recognize a two stage release

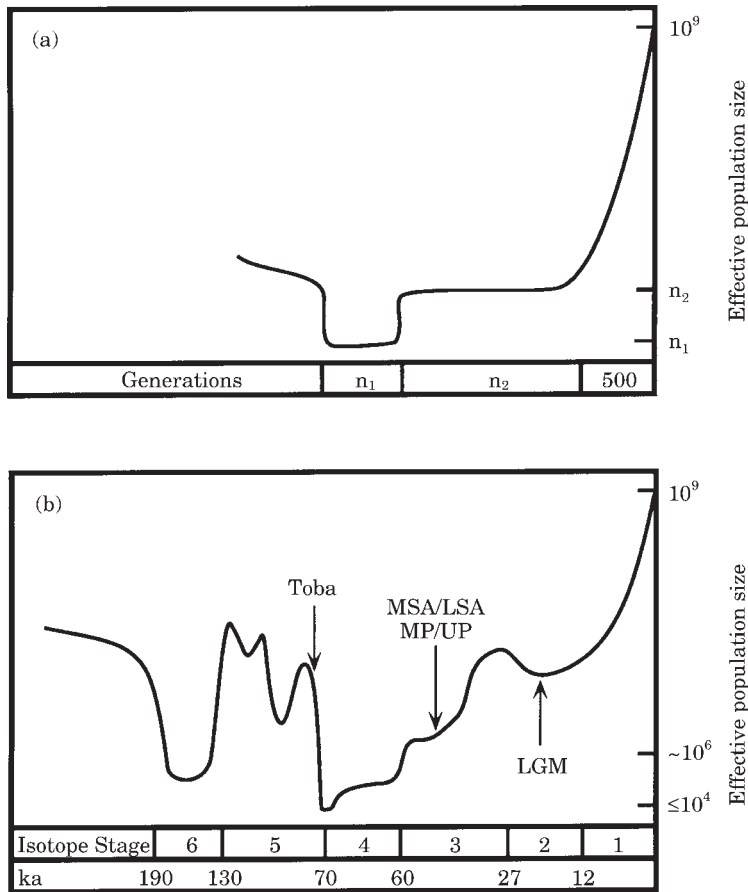


Figure 5. Effective modern human population size through the late Quaternary. (A) The “past history of human numbers” redrawn from Figure 1 in Haigh & Maynard Smith (1972). The spread of food production is mainly responsible for population increase during the Holocene. (B) Revision of Haigh & Maynard Smith’s estimates of effective population size through time, based on genetic, climatic, and archaeological evidence discussed in this paper. Population size may have tracked climate change and primary productivity. Population size was lowest during volcanic winter, but may have remained relatively low throughout oxygen isotope stage 4. Improved technology and social organization may have permitted increased population size after 50 ka and buffered the effects of severe climate on population size.

from the bottleneck in human genetic data? The archaeological evidence discussed above suggests that population densities in more arid areas of Africa remained relatively low throughout the last Glacial MSA/MP and early LSA/UP (Butzer, 1988; Wendorf & Schild, 1992). Relative frequencies of late MSA and early LSA sites in equatorial Africa do not seem to increase, so a significant population release due to technology at the MSA/LSA boundary cannot be demon-

strated. However, chronological resolution of this crucial time period is very poor because there are few reliable techniques of chronometric dating of this period (Ambrose, 1998) and few sites have been excavated.

Anatomically modern humans during the MP/MSA appear to have been less effective in exploiting resources and responding to environmental changes than behaviorally and technologically modern humans of the

UP/LSA (Ambrose & Lorenz, 1990; Klein, 1989a, 1989b, 1992). The effects of volcanic winter and isotope stage 4 on early *anatomically* modern human populations may have been much greater than the effects of the LGM on *behaviorally* modern humans.

The last dispersal of modern humans and/or their technology from Africa may have occurred during isotope stage 3, ~47 ka. Although this may have coincided with, and may have been facilitated by a long, warm interstadial event (D-O interstadial 12) (Dansgaard *et al.*, 1993), it was not accompanied by a significant northward shift of Afro-Arabian biomes (Tchernov, 1992a, 1992b), which suggests modern humans with advanced LSA/UP technology had greater tolerance of cold conditions. Did humans also experience a bottleneck during the LGM? Modern humans thrived in the Last Glacial Maximum (isotope stage 2) environments of many parts of the Old World (Gamble & Soffer, 1990; Soffer & Gamble, 1990), so population densities were probably not substantially lowered during stage 2, despite harsh climatic conditions.

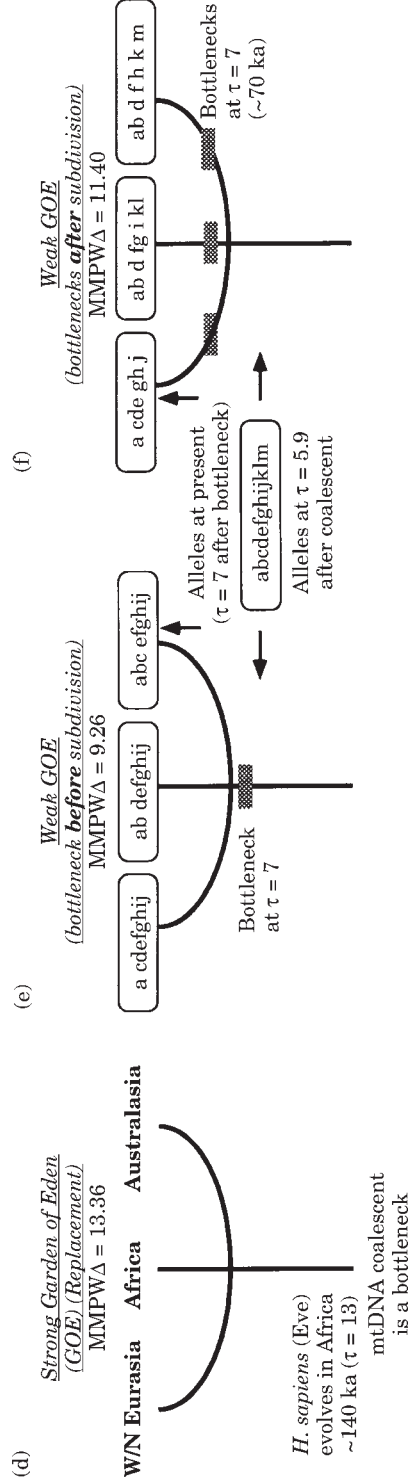
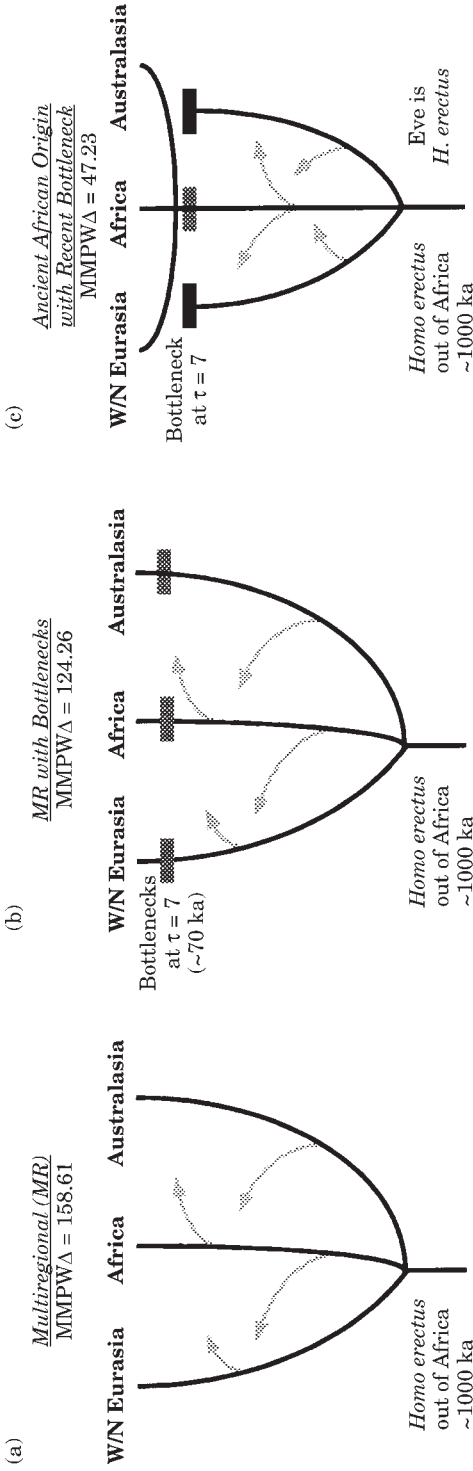
As noted above, chimpanzees apparently experienced a bottleneck at the LGM (Goldberg, 1996). Unless chimpanzees evolved substantially improved adaptability to cold environments between 70 and 20 ka, they may have been much more susceptible than modern humans to climate-related population fluctuations at the LGM. The identification of a bottleneck ~67 ka in the genetic structure of chimpanzee populations in a Pleistocene core refugium in eastern Africa synchronous with that of humans (Rogers & Jorde, 1995; Goldberg, 1996) suggests Toba's volcanic winter may have affected the population history of many species adapted to warm and humid environments. Southeast Asian primates appear to have been greatly affected by climate change at the beginning of the last two

glacial periods (Brandon-Jones, 1996). The genetic structure of primate populations in Asian core refugia should also evince a severe bottleneck around 70 ka.

The effect of bottlenecks on modern human variation

The parent population of the African mitochondrial Eve may have lived as late as 130–140 ka (Stoneking *et al.*, 1992) and all living mtDNA lineages can be traced to her. Low genetic diversity in living human populations is thus largely attributable to the recent origins of modern humans. How much of our current low genetic diversity within, and difference between populations, can be accounted for by our recent African origin *vs.* subsequent bottlenecks in dispersed populations? Alan Rogers (personal communication) has addressed this question by performing computer simulations using his MMGEN program to estimate the mean number of pairwise differences expected under variations of Multiregional, Replacement (Strong GOE) and Weak GOE models, with and without bottlenecks. His results of 1000 iterations of each scenario are illustrated in Figure 6 and explained in Appendix 1.

The Multiregional model [Figure 6(a)] produces a global mean of mean pairwise differences (MMPWΔ) an order of magnitude larger than observed in modern humans (159 in the MR model *vs.* ~12 in extant populations). Recent bottlenecks in three ancient populations [Figure 6(b)] apparently have little effect on MMPWΔ. However, if only one ancient population survives a bottleneck [Figure 6(c)], MMPWΔ is reduced to 47.2, which is still far in excess of that observed in living populations. Our African Eve, who represents the coalescent of all living mtDNA lineages (Cann *et al.*, 1987), is a bottleneck by definition. Simulating a population history of subdivision around 70 ka without



bottlenecks, produces a global MMPWA of ~ 13.4 [Figure 6(d)]. The Weak GOE, with a single bottleneck in Africa before subdivision into three populations, reduces global MMPWA to 9.3 [Figure 6(e)]. Modeling the Weak GOE with bottlenecks occurring after subdivision is closest to the scenario proposed in this paper and implied by Harpending *et al.* (1993). The resulting MMPWA of 11.4 [Figure 6(f)] is most similar to that actually observed, but may not be significantly different from the result of simulation of a single bottleneck prior to subdivision [Figure 6(e)]. Rogers' simulations of Weak GOE scenarios generates MPWA values close to those actually observed in modern humans, but very far from those expected in the Multiregional model (Manderscheid & Rogers, 1996).

Total genetic diversity is reduced by a bottleneck and diversity within subdivided populations is reduced as well. Figure 6(e) shows that if a bottleneck occurs before subdivision, each population will share a large proportion of alleles. However, if bottlenecks occur after subdivision, each one should retain a different subset of the preexisting pool of genetic variants [Figure 6(f)]. In this case within-population diversity is also reduced, but between group differences should increase. Simultaneous decrease in total genetic diversity and increase in between-population difference may seem counter-intuitive, but can be

easily comprehended by an alternative description of the hypothetical Weak GOE scenarios of Figures 6(e) and 6(f). If a single population has 13 alleles (a-m) and passes through a bottleneck before subdivision [Figure 6(e)] the subdivided populations may share 8 of 9 alleles ($\sim 10\%$ difference), because they all lost the same alleles (k-m) through the bottleneck. Differences between populations are due to post-bottleneck loss or gain of alleles. If bottlenecks occur after subdivision [Figure 6(f)], fewer original alleles may be retained in each population, but all of the original alleles may be present among them because the same alleles are unlikely to be eliminated in each population. Between-population difference would increase to $\sim 30\%$. The terms diversity and difference are often used interchangeably, but they should be used to describe total number of alleles and proportions shared, respectively.

The recent African Replacement model, and the Weak GOE with a bottleneck before subdivision [Figures 6(d) and 6(e)] both imply all living human populations should strongly resemble Africans. Bottlenecks after subdivision [Figure 6(f)] may resolve the central, but rarely stated paradox of the Replacement model presented by the apparent magnitude of superficial physical differences between modern populations that are commonly used to classify us into human races: How can modern human races look so

Figure 6. Illustration of Alan Rogers' (personal communication) simulations of mean pair-wise differences in mtDNA sequences of human populations for six models of modern human origins. Simulation assumptions and parameters for each scenario are described in Appendix 1. (A) Multiregional Evolution (MR); (B) MR with recent bottlenecks in each region; (C) Ancient African origin with recent Replacement of non-African populations after a bottleneck; (D) Strong Garden of Eden (recent replacement by recently-evolved Africans) with no bottleneck. The coalescence of mtDNA lineages at the African Eve (~ 130 – 140 ka) is a bottleneck by definition because $MPWA=0$ at the species origin; (E) Weak Garden of Eden (recent replacement by Africans) with one bottleneck prior to subdivision and dispersal; (F) Weak GOE with bottlenecks in each population after subdivision and dispersal. Allelic diversity before and after bottlenecks in E and F is indicated by the letters within rectangles. In E, overlap between populations is high but total MPWA is low because all populations lost the same alleles (k, l & m) during the bottleneck, before subdivision. In F, each population retained a different subset of the pre-bottleneck gene pool so within group diversity is low. However, total MPWA is high because all alleles present before the bottleneck are found among the post-bottleneck populations. Gene flow, assumed for all models, is indicated by stippled arrows in A–C but omitted in D–F for clarity of presentation.

different if we are all such recent descendants of Africans? In other words, if we are all so recently out of Africa, then why don't we all look more like each other and more like our African ancestors?

I propose that smaller, isolated African populations that did survive Toba's volcanic winter in refugia within and/or outside Africa may have experienced the equivalent of the Founder Effect (Mayr, 1970; Nei *et al.*, 1975; Dobzhansky & Pavlovsky, 1953). When populations are reduced to very small sizes, most genetic diversity is lost. A small, random subset of pre-existing genetic diversity is retained in each isolated population. If founder populations remain small and isolated for many generations, then genetic drift leads to the random loss of additional alleles and fixation of others, reducing genetic diversity and increasing between-population difference even further. Additional differentiation can occur through adaptations to local environments. If the Toba super-eruption and hyper-cold millennium between D-O event interstadials 19 and 20 kept human populations small and restricted to isolated refugia, then these processes could have operated for about 40 generations (assuming 25 years per generation). It is highly improbable for several isolated populations to retain the same complement of alleles through bottlenecks [Figure 6(f)]. Therefore the bottleneck could have decreased global genetic diversity while increasing genetic difference between subdivided populations. Evolutionary change occurs fastest in small isolated populations. Therefore population differentiation may have accelerated around 71–70 ka. Without the bottleneck there would have been less interregional difference and more clinal variation across the Old World. We would all look more like Africans. If modern human regional population differences originated in isolated regions during the bottleneck then patterns of clinal variation observed in extant

human populations may be due to gene flow *after* the bottleneck.

Volcanic winter may have inserted a brief Punctuated Equilibrium event (Eldredge & Gould, 1972) (perhaps an exclamation point!) in the course of recent human evolutionary history, accelerating geographic differentiation. This bottleneck may resolve the paradox of why modern human populations look so different from each other yet have such a recent African origin.

Summary and conclusions

Geneticists have repeatedly observed that modern human populations passed through very small population bottlenecks during the early Upper Pleistocene. A possible cause of bottlenecks among genetically isolated human populations is a six-year long volcanic winter and subsequent hyper-cold millennium resulting from the cataclysmic super-eruption of Toba, Sumatra, 71 ka. This dramatic climatic event has not yet been carefully studied with a diverse range of materials and scientific methods; further research is needed to fully evaluate the magnitude of Toba's volcanic winter on global climate and its ecological impacts on humans and other species.

Population expansion following the bottleneck may have occurred in response to climatic amelioration. The alternative hypothesis, that population growth was fueled by improved technology with the invention of modern human technology and behavior at the beginning of the LSA/UP in equatorial Africa, can only be confirmed or rejected after much more archaeological research and an intensive program of accurate chronometric dating.

Volcanic winter is hypothesized to have played an important role in human differentiation during the Upper Pleistocene. Combined with the founder effect, genetic drift and adaptation to local environments, the bottlenecks may account for part of the

overall low human genetic diversity, and between population differences in the superficial physical characters associated with different geographic races. One consequence of volcanic winter may have been rapid differentiation of small, isolated African immigrant populations into modern human races only 71–70 ka. The bottleneck resolves the paradox of the Out of Africa Replacement model: why do human populations look so different yet have such a recent African origin? When the modern African human diaspora passed through the prism of Toba's volcanic winter, a rainbow of differences appeared.

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Appendix 1

Parameters for simulations of mean pairwise differences (MPWΔ) in mtDNA sequences of human populations under different models of modern human origins (Figure 6) generated by Alan Rogers (personal communication). Simulations were run using MMGEN version 3.7 written by Rogers (see Rogers, 1992, 1995; Rogers & Harpending, 1992; Rogers & Jorde, 1995; Manderscheid & Rogers, 1996; Harpending *et al.*, 1993; Sherry *et al.*, 1994). Pairwise distributions were generated from a sample of 50 individuals in each subpopulation, so MPWΔ for each iteration is calculated on a sample of pairwise comparisons between 150 individuals. The formula for number of pairwise comparisons is

$$n(n-1)/2, \quad (1)$$

so for 50 individuals there are 1225 pairwise comparisons. Simulations of mean pairwise differences were repeated 1000 times for each model and the mean of mean pairwise differences (MMPWΔ) for the global population was calculated. The mutation model used by Rogers assumes a finite number of sites in which mutations can occur (finite-flat, sites=360). Model F is most similar to the scenario of population history proposed by Harpending *et al.* (1993) and produces an MMPWΔ closely similar to that observed in modern humans (~12).

The mathematic definitions of the parameters used can be obtained in the references cited above. The two most important parameters (quoted from Sherry *et al.*, 1994: 762) “are

$$\theta = 2Nu, \quad (2)$$

the conventional product of female effective population size N and the locus-specific mutation rate u (per generation); and

$$\tau = 2tu \quad (3)$$

the date of expansion measured in units of mutational time, where t is time in generations." Generation length is 25 years.

The table below describes the conditions for each scenario illustrated in Figure 6. Gene flow (mn) is number of individuals per generation and K is the number of populations surviving during time τ . There is no gene flow during bottlenecks. The simulations do not specify the age of Eve. In each simulation, Eve's age is a random variable,

and Eve's age is likely to be different in each simulation. In models D–F, Eve's population grows from a small size ($\theta=1$) at $\tau=13$ before present. Assuming mutation rates determined by Stoneking *et al.* (1992), $\tau=13$ is equivalent to ~ 130 – 140 ka. Bottlenecks are set to begin at $\tau=5.9$ after Eve (~ 71 ka), to persist for $\tau=0.1$ (~ 1000 yr) and to end at $\tau=7$ before present (~ 70 ka). The first line of each model's parameters is the most recent set of conditions in the population history scenario.

Appendix

Model	θ	mn	τ	K	MMPWA
A. Multiregional evolution (MR), with no bottlenecks	1000.0	0.1	infinite	3	158.61
B. Multiregional, with recent bottlenecks in three populations	1000.0	0.1	7.0	3	124.26
	0.1	0.0	0.1	3	
	1000.0	0.1	infinite	3	
C. Ancient African Eve, with a recent bottleneck and extinction of two non-African lineages	1000.0	0.1	7.0	3	47.23
	0.1	0.0	0.1	1	
	1000.0	0.1	infinite	3	
D. Strong Garden of Eden (recent origin and replacement). No bottleneck after origin of <i>H. sapiens</i> . The coalescent (Eve) is a bottleneck	1000.0	0.1	13.0	3	13.56
	1.0	0.0	infinite	1	
E. Weak Garden of Eden, with a recent bottleneck in Africa <i>before</i> subdivision into three populations	1000.0	0.1	7.0	3	9.26
	0.1	0.0	0.1	1	
	1000.0	0.1	5.9	3	
	1.0	0.0	infinite	1	
F. Weak Garden of Eden, with recent bottlenecks <i>after</i> subdivision into three populations	1000.0	0.1	7.0	3	11.73
	0.1	0.0	0.1	3	
	1000.0	0.1	5.9	3	
	1.0	0.0	infinite	1	