Palaeoclimates, plasticity, and the early dispersal of *Homo sapiens*

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Abstract

The origin and initial dispersal of *Homo sapiens* out of East Africa and into the Levant remains a major research focus in evolutionary anthropology. There is little doubt that climatic changes played a role in facilitating this dispersal, but the specific dynamics remain poorly understood. This contribution surveys the fossil and genetic evidence for the origin and dispersal of modern humans, and situates this evidence within the context of biological theories of plasticity and dispersal. It is shown that certain climatic and environmental conditions are expected to lead to the evolution of plastic strategies, and that such strategies are characteristic of successfully dispersing species. A model is formulated that allows for the identification of features in climatic records that are conducive to the evolution of plasticity, and thus to the development of dispersal capabilities. Using as an example a palaeoclimatic record from Lake Tana, Ethiopia, the model is used to pinpoint the chronology of likely periods of dispersal from East Africa. Results indicate the presence of a dispersal phase c.97-105ka, a date that fits well with the initial modern human colonisation of the Levant shortly after 100ka. Implications of recent genetic chronologies for the origin of non-African modern humans and the archaeological evidence for possible routes out of Africa are discussed in this context.

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1. Introduction

The timing and causes of *Homo sapiens* dispersal out of Africa remain major foci of research in evolutionary anthropology. Climate has long been considered to play a substantive role in hominin dispersals, and the publication of a growing number of well dated, high resolution palaeoclimatic records makes the production and testing of climatically driven dispersal hypotheses an increasingly valuable endeavour. The fact that the dispersal of *Homo sapiens* is further constrained by an increasing body of genetic data, in addition to the more traditional fossil and archaeological evidence, provides a situation in which the reconstruction of dispersal events is now more tangible and reliable than ever. This wealth of data has also, however, led to the understanding that the dispersal history of our species is far more complicated than had once been imagined, with many researchers now accepting the probability of multiple dispersal events of varying duration and success. A straightforward 'wave of advance' model is now widely considered to be overly simplistic, with more realistic models incorporating multiple dispersal events governed at least partially by the oscillations of Late Pleistocene climates.

Despite recent advances, the nature of the relationship between climate and hominin dispersal remains vague. Most attempts are largely atheoretical, using as a starting point the idea that certain environments are conducive to hominin habitation, and that the existence or spread of such environments will be conducive to hominin persistence or expansion. This is undoubtedly a valid and useful baseline approach, but as our understanding of the interactions between climate, environment, and hominin evolution becomes more highly developed, there is an increasing need for more nuanced, theoretically grounded perspectives on the dynamics of dispersal. Such perspectives must take into account what is known about the relationships between climatic change, climatic variability, and evolution in taxa beyond those of our own lineage. In this respect the biology of adaptation in fluctuating environments has much to offer, though for the most part this extensive literature has failed to permeate research on human evolution. A consistent, recurring relationship between climatic variability and the evolution of phenotypic plasticity or behavioural flexibility (Grove 2011a, 2011b, 2012a, 2012b), as summarised below, is of particular relevance, as are the related paleontological notions of 'habitat theory' (Vrba 1992, 1995) and 'variability selection' (Potts 1998, 2013).

This paper will first review findings from evolutionary biology and related fields that are essential to, but thus far neglected in, reconstructions of the interaction between palaeoclimate and human evolution. Key to these findings is the fact that temporal variability in environments is more likely to lead to the accumulation of plasticity than is spatial variability. The genetic, fossil, and archaeological evidence of hominin dispersals will be considered, with a focus on the first movement of *Homo sapiens* out of East Africa and into the Levant. This dispersal, widely considered to have 'failed' in terms of permanent habitation of the Levant, is of particular interest because of the wealth of fossil and archaeological data, combined with a series of increasingly sophisticated dating efforts. The final section of the paper presents a simple evolutionary model that allows explicit conclusions to be drawn about when plasticity accumulates, how it affects the biological fitness of populations, and when the dynamics of adaptation to climate change would be expected to equip populations with the pre-requisites for dispersal. This model facilitates the formation of a generic theory of hominin dispersals, and has the potential to be used in conjunction with empirical palaeoclimatic datasets. An example of the latter is provided using data from Lake Tana, Ethiopia, and the results are related to the surveyed fossil and genetic data for the origin and early dispersal of Homo sapiens out of East Africa.

2. A Biological Review

The following paragraphs consider the biology of plasticity, particularly as it relates to effects generated by fluctuating environments. This necessitates a definition of plasticity, which is viewed in broad terms here to mean any mechanism by which a population or individual may adapt relatively rapidly to changes in the environment. The speed of adaptation is critical here, since any population could in theory track a changing environment by evolving towards a new optimum given sufficient time, but simple genetic systems experience perpetual lags in moving towards such optima precisely because those optima are themselves constantly changing. If we assume, as per the modelling presented in **Section 4**, that the optimum value of a trait is that which maximises fitness in a given environment, we can simplify matters without being specific as to what precisely the trait is, or how it might be encoded: we simply postulate that animals with a trait value of a will do particularly well under environmental state a, and that they will do worse, or perhaps be non-viable, in environmental state b. Fitness in environmental state b will be measured as some function of the distance $d = |b - a|$, with higher values of d equating to lower fitness. An important aspect of plasticity in this scenario is that it can increase fitness in the regions around a, thus increasing the animal's tolerance of changing environments. It can also, as reported below, allow a population to remain viable under environmental change when non-plastic populations might be driven to extinction and, via the maintenance of phenotypic variation, allow that population to track changing environments at much faster rates.

2.1. Foundations

Beginning with foundational genetic research by Levene, Dempster and others (Levene 1953; Dempster 1955; Haldane and Jayakar 1963; Cohen 1966; Lewontin and Cohen 1969; Gillespie 1974), a long history of findings in evolutionary biology have suggested that temporal fluctuations in the environment are likely to lead to the accumulation of various forms of plasticity. Much of this early research considered the maintenance of genetic polymorphisms or directly related micro-evolutionary concerns, but also provided the basic mathematical axioms that are now considered to govern evolutionary dynamics in fluctuating environments across far broader scales (Simons 2002; Lee and Doughty 2003). In basic terms, the contrast between selection acting on organisms that experience multiple environmental states simultaneously as opposed to those experiencing multiple states sequentially is based on the fact that overall fitness in the former case is measured as the arithmetic mean of the fitnesses in each state whilst in the latter case it is calculated as the geometric mean. The underlying micro-evolutionary logic is that an animal that encounters multiple environmental states in quick succession (≈ simultaneously) will have an overall fitness that is the simple average of its fitnesses in those states. Since the environments do not change over time, this simple average will be identical in each generation; since there will be no variance in fitness between generations, the arithmetic and geometric means over the long-term will be the same, and the long-term result will be determined entirely by the instantaneous result.

Much like population growth, long-term fitness is *multiplicative* rather than additive, and is therefore measured via the geometric mean. If individual A has three times the fitness of individual B it will (on the simplest model) leave three times as many offspring. If the offspring of individual A are also three times as fit as those of individual B, they will themselves leave three times as many offspring. Two generations down the line, the descendents of individual A will be 9 times as numerous (3×3) as those of individual B, not six times as numerous (3+3). The multiplicative nature of long-term fitness becomes a major factor when fitness changes between generations, because the geometric mean is highly sensitive to variance; this leads to the sometimes counter-intuitive finding that low variance in fitness between generations can be more beneficial than high (arithmetic) mean fitness within generations.

Figure 1a shows the tolerances of four populations of similar animals to environmental states between 0 and 10 (these states might be thought of as increments along any continuous axis describing habitat variation, but are probably most usefully viewed as temperatures or moisture levels). We assume none of the populations are viable below state 0 or above state 10. Consider that states 3-7 occur as adjacent (perhaps latitudinal) bands of habitat, and that each is unchanging through time. Population 4 is far more tolerant than the other three species (its distribution has a greater variance, resulting in wider, fatter tails), but this comes at a cost. Since the integrals of all tolerance curves equal 1 (following Levins 1962, 1968), the tolerance curve of population 4 has a much lower peak than those of the other three populations. This has the effect that Population 4 is never the fittest population: Population 3 is fittest in states below 4, Population 2 fittest in states between 4 and 6, and Population 1 fittest in states above 6. This means that, in an evolutionary scenario, Populations 1-3 will partition the environment amongst them, each living in the habitat to which it is best suited, whilst Population 4 will not be able to gain a foothold anywhere. In a scenario in which all four populations are required to experience all environments from 3-7 simultaneously due to, for example, population expansion or habitat destruction, Population 2 will eventually displace the others due to the fact that it has a marginally higher arithmetic mean across the environmental states considered (see Table 1).

However, imagine now an environment that oscillates as per Figure 1b. We now consider the entire area earlier viewed as being composed of latitudinal bands of habitat to be homogenous at any given time. At generation 0 it is all in state 5; it climbs to state 7, falls to state 3, and so on as per Figure 1b. Thus the same range of environments, 3-7, is considered, but now all four populations experience all these environmental states every 10 generations. Whereas in the spatial scenario Population 4 cannot survive anywhere, it is now the only population that can survive anywhere, and fills the entire area. A standard population genetic realization of this outcome, with subpopulations carrying alleles for the mean and SD values of their tolerance curves, is modelled in Figure 1c. Population 4, the most tolerant or plastic population of the four, eventually dominates the area to the exclusion of the other populations because it has the highest geometric mean fitness over environmental states 3-7.

2.2. From polymorphism to plasticity

It takes some further theoretical work, however, to expand the finding that fluctuating climates can lead to the maintenance of polymorphisms (as per Dempster 1955 and Haldane and Jayakar 1963) into a scenario in which plasticity *per se* is favoured in such environments. The genetic polymorphism argument implies that a population maintaining polymorphisms may be tolerant of a wider range of environments, but whilst greater tolerance is necessarily a result of plasticity, the latter implies a particular type of response. To understand this difference we must first understand the distinction between specialism and generalism and, furthermore, the often conflated distinction between stenotopy and eurytopy. Consider three species of canid: A is a cold specialist, B a warm specialist, and C a generalist able to withstand both cold and warm conditions to some extent. A has a relatively thick coat, B a relatively thin coat, and C a coat of intermediate thickness. Note that A, B, and C all follow fixed strategies, and thus that even the generalist is not plastic. Now consider the plastic species D, which grows a thicker coat in colder conditions but sheds this coat if temperatures increase. This plasticity may be developmental in the sense that coat thickness is determined by temperatures experienced during ontogeny, or it may persist into adulthood, with phases of thickening and shedding cued by, for example, seasonal variations throughout the lifetime. It is this latter form of plasticity with which the current paper is primarily concerned. Finally, note that whilst the specialists A and B are stenotopic, both the generalist and the plastic species are eurytopic. Since plastic species are not generalists but are eurytopic, 'eurytopy' and 'generalism' cannot be synonyms. More importantly, stenotopy and eurytopy are descriptions of observable *outcomes*; their Greek roots imply that these outcomes will be seen in the narrower ranges of environments inhabited by stenotopes. Specialism, generalism, and plasticity by contrast are descriptions of the *mechanisms* by which species achieve their distributions.

With the key distinctions established, the full transition from polymorphism to plasticity *per se* can be made via the use of an exceptionally valuable analysis by Moran (1992; see also Sober 1994; Godfrey-Smith 1996). Moran's (1992) argument was originally framed in the context of developmental plasticity but, as other researchers have noted, the analysis is equally well suited to plasticity of any kind (e.g. Sober 1994; Godfrey-Smith 1996). The model again juxtaposes the effects of spatial as opposed to temporal heterogeneity on the evolution of plasticity, postulating the existence of two environments and two possible phenotypes. Crucially, Moran introduces an additional parameter – the probability that an animal will produce the phenotype best suited to the environment it encounters – allowing her to examine continuous regions of parameter space in which plasticity evolves, rather than the dichotomous point estimates of 'plasticity or not' produced by many prior analyses.

What follows is a simplified sketch of Moran's (1992) analysis; interested readers are encouraged to consult the original for fuller details. There are two environments, environment 2 occurring with probability r and environment 1 with probability $(1-r)$. The fitness of an animal producing phenotype 1 in environment 1 (a 'correct' or fitness-maximising match) is $f_{(1,1)}$; the fitness of an animal producing phenotype 2 in environment 1 (an 'incorrect' or fitness-minimizing match) is $f_{(2,1)}$. Similar options and subscripts apply to environment 2. A generalist has fitness $f_{(g)}$ in both environments. We assume a relative fitness scoring of $f_{(1,1)} = f_{(2,2)} > f_{(g)} > f_{(1,2)} = f_{(2,1)}$. Finally, a measures the probability that a plastic animal will produce the phenotype best suited to the environment it encounters. In a spatially varying environment, the fitnesses of two opposed specialisms, w_{s_1} and w_{s_2}, of generalism, w_g, and of plasticity, w_p, are:

$$w_{s_1} = rf_{(1,1)} + (1-r)f_{(1,2)} \quad [1a]$$

$$w_{s_2} = rf_{(2,1)} + (1-r)f_{(2,2)} \quad [1b]$$

$$w_g = rf_{(g,1)} + (1-r)f_{(g,2)} \quad [1c]$$

$$w_p = r\big[af_{(1,1)} + (1-a)f_{(2,1)}\big] + (1-r)\big[af_{(2,2)} + (1-a)f_{(1,2)}\big] \quad [1d]$$

An example of a plot of the model output using $f_{(1,1)} = f_{(2,2)} = 1$, $f_{(1,2)} = f_{(2,1)} = 0$, and $f_{(g)} = 0.5$ for values of r and a from 0 to 1 is shown in Figure 2a. Note that such graphs are utilised by plotting the fitnesses w_{s_1}, w_{s_2}, and w_g for the given values of r, and then reading off the values of a that would be sufficient to provide a fitness advantage for the plastic strategy over all other strategies. [These are the values of a that occur between the highest (=fittest) line describing any other strategy for a given r value and the top of the graph.] Figure 2c clarifies the regions of the graph favouring particular strategies.

Figures 2a and 2c demonstrate that plasticity is most likely to evolve when environments 1 and 2 are equally likely to occur, as this prevents either of the specialist strategies dominating. Regardless of the balance of environments, a must be greater than 0.5 for plasticity to evolve. This is perfectly logical condition, as with two environments and two phenotypes the probability of matching phenotype to environment by random chance is 0.5; thus the plastic strategy must simply be better at matching than random chance. As per the analysis described above and graphed in Figure 1, there is no niche for a generalist under conditions of spatial variability. Switching from spatial to temporal variation in Moran's (1992) model, and thus from arithmetic to geometric means, yields a new set of equations:

$$w_{s_1} = {f_{(1,1)}}^{r} \cdot {f_{(1,2)}}^{(1-r)} \quad [2a]$$

$$w_{s_2} = {f_{(2,1)}}^{r} \cdot {f_{(2,2)}}^{(1-r)} \quad [2b]$$

$$w_g = {f_{(g,1)}}^{r} \cdot {f_{(g,2)}}^{(1-r)} \quad [2c]$$

$$w_p = \big[af_{(1,1)} + (1-a)f_{(2,1)}\big]^{r} \cdot \big[af_{(2,2)} + (1-a)f_{(1,2)}\big]^{(1-r)} \quad [2d]$$

Graphs of the model, using the same f values as before, are shown in Figures 2b and 2d.

Temporal variability causes considerable changes to the sizes of the regions available to the four strategies (compare Figures 2c and 2d). The regions available to the two specialists decrease considerably, whilst the region available to the plastic species increases, and a large region in which generalism is favoured also appears. Importantly, the region of the graph favouring plasticity is now the largest single region, demonstrating the likelihood of plasticity evolving under temporal variability in climate.

The value of Moran's (1992) model and of other, subsequent models of similar structure (Sober 1994, Godfrey Smith 1996) is that they provide a highly generic picture of the conditions under which plasticity can evolve, without being tied to a particular scale (i.e. alleles at a locus, or individuals in a population). This wide applicability is shown by the fact that Sober (1994) uses a mathematically equivalent model to predict the environmental conditions under which learning would be favoured over what he dubs '*a priori* prejudice' (this being the equivalent of a fixed specialism above). Such models simply demonstrate the highly generic, cornerstone principle that *temporal variability in climate is more likely to lead to the evolution of plasticity than is spatial variability in climate*.

2.3. Plasticity and dispersal

Plasticity, then, is highly likely to evolve under conditions of temporal variability in climate, but what does the presence of such plasticity imply for the ability of a species to disperse? Beginning with seminal papers by Mayr (1965) and Baker (1965, 1974), evolutionary biologists have spent considerable time compiling lists of traits common to those species of plants, birds, and animals that have demonstrated the propensity for successful dispersal or invasion. All such trait lists have included plasticity or related metonyms. Baker sees successful invaders as possessing "general-purpose genotypes" (Baker 1965:166) or the tendency towards "wide environmental tolerance" (Baker 1974:6). Two of Mayr's six characteristics of colonizing species – "considerable ecological flexibility" and the "ability to shift habitat preference" (Mayr 1965:40-41) – are an analogue and a potential result of plasticity, respectively. As discussed above in consideration of the Moran (1992) model, such plasticity is often discussed in general terms, rather than being presented as the result of a specific mechanism.

Potts (1998), in presenting the 'variability selection hypothesis', discusses both polymorphism and phenotypic plasticity as potential means of achieving what he terms 'adaptive flexibility' (Potts 1998: 84ff.). Potts' primary concern however, is with the attainment of flexibility through the evolution of "complex structures or behaviours that are designed to respond to novel and unpredictable adaptive settings” (Potts 1998:85). Crucially, this occurs as populations confront “highly variable environments over many generations” (*ibid*.), and is thus consistent with the modelling approach adopted below. As a theoretical example of a potential result of variability selection, Potts (1998) suggests a novel foraging strategy that allows a population to spread into a new environment, utilising a newly available food type. Flexible responses to novel situations are thus at the heart of variability selection, and are endorsed here as a primary result of plasticity. Indeed, some of the most fruitful recent research on the relationship between plasticity and dispersal success has been based on behavioural flexibility underlain by a variety of mechanisms including tendencies to neophilia, innovation, and learning (e.g. Sol 2003, 2007).

In his trait list of attributes characterising successful invaders, Sol (2007:133) harks back to Baker and Mayr, including high values of both niche breadth and behavioural flexibility. The niche breadth hypothesis has become the modern crystallization of Mayr’s (1965) research, with Vázquez (2006) providing a literature review demonstrating its prevalence in successfully dispersing species. His review (Vázquez 2006) suggests that native habitat, geographic, or climatic range are good predictors of success, with work on birds by McLain and colleagues (1999) and Cassey and colleagues (2004) suggesting that habitat or dietary breadth are of particular importance. Heterogeneity of habitats would seem the likeliest driver here, with geographic range showing positive results simply because large ranges are, on average, more likely to contain a diverse array of habitats than are smaller ranges. The average size of the individual home range within a species, however, may also be a useful predictor of potential dispersal speed, as wide-ranging individuals are necessarily more mobile than those with small home ranges. Greenberg and Mettke-Hofmann (2001) find that behaviourally flexible species are more likely to be neophiles, with Sol’s (2003) analysis suggesting that generalism and flexibility also tend to correlate.

The issues of neophilia and innovation touch directly on the two primary – and contradictory – hypotheses of the evolutionary effects of behavioural plasticity. The hypothesis of behavioural drive (Hardy 1965; Wyles et al. 1983) asserts that when behavioural plasticity leads populations to spread into areas beyond their native habitats, it also exposes them to new selection pressures, and may thus increase evolutionary rates. Conversely, the hypothesis of behavioural inhibition (Bogert 1949; Huey et al. 2003) asserts that since behavioural plasticity enables populations to inhabit varied environments *without* underlying genetic change, it must necessarily reduce evolutionary rates. Wyles and colleagues (1983) suggested that high rates of evolution in songbirds (measured as morphological distance per unit time, relative to other birds) are due to their ability to innovate and socially transmit novel behaviours. They also found strong correlations between rates of evolution and brain size, and argued that encephalisation supports the propagation of behavioural innovations (see also Hardy 1965). This opens new niches for larger brained species, exposing them to novel selection pressures, and thus increasing evolutionary rates. This canonical example of behavioural drive is countered by evidence from Bogert (1949). The latter found that the same species of lizard subjected to different temperature regimes could thermoregulate via behaviour (e.g. basking more often in cooler environments); he thus concluded that behavioural flexibility can negate the need for specific adaptations to geographical or altitudinal temperature clines, and can thus slow evolutionary rates. These two hypotheses reduce to a simple but crucial difference in stimulus: whilst both assume selection is driven primarily by changes in environment, behavioural drive suggests that exposure to those changes is the result of behaviour, and thus that behaviour rather than environmental change itself is the driver of evolutionary change. With the renewed focus in recent years on the role of behaviour in evolution (e.g. Odling-Smee et al. 2003), the relationship between these two hypotheses has been brought into sharper focus.

Finally, a theory directly linking dispersal success to the geometric mean argument seen in the work of Moran (1992) and others involves the concept of 'fitness homeostasis' (Rejmánek 2000). This theory suggests that the function of behavioural plasticity is to effectively equalize fitness across a wide range of environments; in this sense, such plasticity acts as a buffer between environmental heterogeneity and fitness, ensuring that relatively high fitness is maintained even in non-native or marginal environments. According to this theory, plasticity would considerably reduce the variance in fitness experienced by an individual, and would therefore increase its geometric mean fitness relative to that of a less plastic individual. Of particular interest in this context are two recent studies that hint at the potential for plasticity to lead to fitness homeostasis and survival of populations of birds and arthropods under the pressures of anthropogenic climate change (Chown et al. 2007; Charmantier et al. 2008). The findings of Chown and colleagues (2007) are notable in that they suggest that invasive species are more resistant to climate change than are indigenous species, further highlighting the link between plasticity and dispersal success.

3. The chronology of hominin dispersals

The general chronology of hominin dispersal is based on the idea of two primary dispersals from Africa, the first of *Homo erectus sensu lato* after 2Ma and the latter of *Homo sapiens* after 100ka. It is now widely understood that the two 'Out of Africa' events form what is really just a useful heuristic for examining a far more complex and nuanced series of dispersal events, heavily influenced by climate, over the past two million years. The role of Asia as a potential source of, rather than purely a destination for, dispersing hominins has become an increasingly intriguing debate in recent years (e.g. Petraglia et al. 2007; Armitage et al. 2001; Rose et al. 2011; Boivin et al. 2013), further questioning the simplicity of the Out of Africa model. Whilst the focus here is strictly on the earliest dispersal of *Homo sapiens* out of East Africa and into the Levant, a brief, selective review of earlier dispersals is of interest in terms the literature on plasticity and dispersal. The following paragraphs thus discuss *Homo erectus sensu lato* dispersals before focusing in some detail on the origin of *Homo sapiens* in East Africa and the chronology of this species' dispersal into the Levant.

3.1. Early hominin dispersals

Homo erectus, the first hominin species to disperse beyond Africa, was established in East Africa by shortly after 2Ma, is found in the Caucasus and Java by 1.8Ma, in China by 1.6Ma, and in Israel by 1.4Ma (Gabunia et al. 2000; Swisher et al. 1994; Zhu et al. 2004; Tchernov 1995). This species had reached mainland Europe by around 0.8Ma, and Britain by at least 0.78Ma (Bermudez de Castro et al. 2004; Parfitt et al. 2010). *Homo erectus* has been characterised as a 'widespread, polytypic' species (Rightmire 1995); no other hominin species endured for as long, and only *Homo sapiens* has surpassed its geographical extent. Even when employing a splitting taxonomy *Homo erectus* is a morphologically variable species, and the current debate surrounding Skull 5 from Dmanisi (Lordkipanidze et al. 2013) may require an admission of even further variability. Its larger brain and almost modern stature might both have equipped it for rapid dispersal, as might its perceived dietary and habitat generalism (Robinson 1954; Jolly 1970; but see Wood and Strait 2004; Strait et al. 2013). The Acheulean technology with which it is primarily associated in Africa might have both facilitated dietary breadth and enabled the more efficient processing of animal foods. For example, although Oldowan hominins were able to process faunal bone marrow to some extent (e.g. Madrigal and Blumenschine 2000; Blumenschine and Pobiner 2007), handaxes might have been more appropriate tools for the splitting of long bones (e.g. Pante 2013).

3.2. The origin of Homo sapiens

Like *Homo erectus*, *Homo sapiens* first appeared in East Africa. A number of early sites dating to after 200ka give an impression of the origin and spread of the species within the region, though many of the individual specimens are morphologically transitional, retaining archaic features alongside the hallmarks of biologically modern humans. Furthermore, there is considerable morphological variability between 200ka and 100ka in the region, with even apparently contemporaneous crania showing marked differences in their degree of modernity (the relatively modern Omo I and relatively archaic Omo II being the best example of the latter). Bräuer (1984, 2008, 2012; Bräuer et al. 1997) has developed a useful three-grade taxonomy, organising this material into Early Archaic, Late Archaic, and Modern *Homo sapiens* based on cranial features. Early Archaics possess *Homo sapiens* features such as reduced supraorbital and occipital tori, more vertically oriented lateral walls and an expanded frontal, with resulting increases in cranial capacity. Late Archaics continue these trends, but also have apomorphic facial features including canine fossae and inframalar curvature (Bräuer 2008; see also Mbua and Bräuer 2012). This taxonomy continues to be revised due to re-dating and examination of new and existing specimens, but provides a useful reference point for the following paragraphs.

Ethiopia is by some distance the country most likely to contain the geographical origin of anatomically modern *Homo sapiens*, with the sites of Omo and Herto being the strongest candidates. The Herto specimens are chronologically very well constrained to between 160±2ka and 154±7ka via dates on the surrounding sandstone and a capping tuff (Clark et al. 2003), whilst the age range for the Omo fossils is considerably broader, bracketed by the Aliyo and Nakaa'kire tuffs at 104±1ka and 196±2ka, respectively (McDougall et al. 2005, 2008; Brown and Fuller 2008). A later minimum age for the Omo fossils has been argued based on a proposed correlation of the deposition dates of the members of the Kibish Formation with those of the east Mediterranean sapropels (McDougall et al. 2008). If this correlation is causal, with the members of the Kibish Formation forming rapidly during the same wet phases as the sapropels, the minimum age of Omo I and II would be 172ka, based on the formation of the overlying layer during the same phase as eastern Mediterranean Sapropel 6 (Lourens et al. 1996; McDougall et al. 2008).

Morphologically, White and colleagues (2003) consider the Herto hominins to represent a new subspecies, *Homo sapiens idaltu*, intermediate between Late Archaic and anatomically modern *Homo sapiens*, further suggesting that it is the immediate ancestor of the latter. The archaeology is also transitional, showing Acheulean elements such as fine-grained basalt handaxes in addition to the dominant Levallois component including the production of points on obsidian. Bräuer (2008) considers Omo I to be anatomically modern and Omo II to be Late Archaic, despite their probable contemporaneity (see McDougall et al. 2008; Brown and Fuller 2008; Brown et al. 2012). This apparent anomaly is a prime example of the fact, often stated in analyses of putative *Homo sapiens* crania, that the modern human anatomical mosaic appears piecemeal, with both geographical and temporal trends being apparently discontinuous at the scale of analysis permitted by the specimens available. Elsewhere in Ethiopia, and somewhat later, four hominin crania from Aduma and a further right parietal from Bouri, around 10km to the southeast, date to between 84ka and 105ka (Haile-Selassie et al. 2004; Yellen et al. 2005). The relatively complete ADU-VP-1/3 cranium from Aduma is considered to show some Late Archaic features, but is essentially modern (Haile-Selassie et al. 2004:9).

Beyond Ethiopia, East African early *Homo sapiens* material comes primarily from Kenya, Tanzania, and Sudan; the relevant fossil localities are surveyed briefly here. From Kenya, the most chronologically relevant specimens are the Late Archaics from Eliye Springs (the ES-11693 cranium) and Ileret (the KNM-ER 3884 cranium and KNM-ER 999 femur). The former is from the West Turkana area but lacks a clear stratigraphic context, being generically assigned to the period between 200ka and 300ka (Bräuer and Leakey 1986). It has morphological affinities to Omo II and Laetoli 18, but also shows more primitive features characteristic of the Early Archaics from Eyasi and Ndutu (Bräuer and Leakey 1986; Bräuer 1989). The very thick cranial vault, once considered a primitive trait, is now regarded as being a pathological alteration due to chronic anaemia (Bräuer et al. 2003). The Ileret cranium is considered Late Archaic, though a number of modern features lead Bräuer and colleagues (1997) to suggest that it is a possible transitional form between Archaics and Moderns. These authors also find similarities between KNM-ER 999 and the femoral sample from the Israeli sites of Qafzeh and Skhul (see below). Both KNM-ER 3884 and KNM-ER 999 are thought to date to between 270 and 300ka.

Tanzania has also provided a rich fossil record for the study of modern human origins, with specimens from Eyasi, Mumba, and Laetoli all contributing to the debate. A U-series date on the overlying Mumba Beds gives a minimum age for the three Lake Eyasi crania of 131ka (Mehlman 1987). Based on morphological analyses of the most complete cranium (EH01), faunal and archaeological analyses (Mehlman 1984, 1987), and local geology, Bräuer and Mabulla (1996) conclude that the Eyasi hominins are of Middle Pleistocene date, probably between 200 and 400ka. EH01 is morphologically similar to other East African fossils such as those from Ileret and Eliye Springs, as well as Laetoli 18; it is thus transitional between Early and Late Archaics (*sensu* Bräuer 2008). An additional hominin frontal bone from Lake Eyasi, designated EH06, was reported in 2008 (Domínguez-Rodrigo et al. 2008). EH06 is morphologically similar to EH01, but is dated via ESR and U-series to between 88ka and 132ka, leading Domínguez-Rodrigo and colleagues (2008:903) to argue that archaic features may have persisted relatively late in the region.

The chronologically late but morphologically primitive EH06 provides an interesting counterpoint to the ‘unequivocally modern’ material from Mumba Rock Shelter, just over three kilometres away from Eyasi (Bräuer and Mehlman 1988). Dated by Uranium-Thorium to at least 125ka, the three molars comprising Mumba XXI are of a similar age to EH06, but if their modern attribution is correct they are indicative of a very different morph. Also of similar age is LH18, from the Ngaloba Beds at

Laetoli (Day et al. 1980; Magori and Day 1983), dated via uranium-thorium on associated animal bones to 129±4ka (Hay 1987). This fragmented cranium is considered to show a mosaic of archaic and modern features, with similarities to both EH06 and Omo I (Magori and Day 1983; Bräuer 2008).

Finally, the important Singa calvaria from Sudan appears to be at or the near the morphological boundary between Late Archaic and Early Modern *Homo sapiens* (Stringer et al. 1985; McDermott et al. 1996; Spoor et al. 1998). Though Stringer (1979) stressed the archaic elements of the specimen, McDermott and colleagues view Singa as representing "an African population that immediately preceded the appearance of *H. sapiens* in Africa and in the Levant" (McDermott et al. 1996:515). The mixture of modern and archaic morphology, together with pathological features identified via CT scans (Spoor et al. 1998) make Singa an enigmatic specimen, and uranium-thorium dates suggesting the calvaria pre-dates 133ka also suggest that it may be important in the piecemeal evolution towards anatomical modernity.

3.3. Early Homo sapiens *in the Levant*

Whilst arguments over which *Homo sapiens* fossils are the earliest within Africa remain to be resolved, there is no doubt that the earliest members of our species to leave Africa are represented by the skeletal material from the Israeli cave sites of Qafzeh and Skhul. Indeed, well dated fossils of *Homo sapiens* outside Africa and the Levant do not appear until ≈45ka, despite probable archaeological indicators of modern human presence in some areas well before this date (see Boivin *et al*. 2013). As the current paper focuses on the climatic background to this earliest appearance of modern *Homo sapiens* outside Africa, the following paragraphs discuss the material from Qafzeh and Skhul in some detail, focusing on the considerable efforts that have been given to the dating of the deposits. Although Qafzeh and Skhul are considered by the majority of researchers to represent a short-lived and ultimately unsuccessful early dispersal event (e.g. Shea 2003, 2008; Mellars 2006), with modern humans replaced by Neanderthals in the Levant after c.70ka, a combination of the wide date ranges on these two sites and recent genetic analyses dating the timing of the dispersal event leading to all non-African *Homo sapiens* show that there is considerable ambiguity surrounding this conclusion. The genetic evidence is addressed in detail in section 3.4.

3.3.1. Qafzeh

Qafzeh cave, near Nazareth in Lower Galilee, Israel, was excavated by Neuville and Stekelis from 1932-5 and by Vandermeersh from 1965-79 (Vandermeersh 1981). The five complete burials and fragmentary remains of up to 11 other individuals from layers XV and XVII show some primitive features (Stringer and Trinkaus 1981), but are unequivocally modern humans. Dates are provided by

Valladas et al. (1988), Schwarcz et al. (1988), McDermott et al. (1993), and Yokoyama et al. (1997). Valladas et al. (1988) provide thermoluminescence dates on 20 burnt flints; those on layer XVII, from which hominins 8-12 and 14-17 were recovered, date to between 87.8 ± 7.2ka and 107.2 ± 8.8ka, with the overall range of dates on layers XVII to XXIII spanning 82.4 ± 7.7ka to 109.9 ± 9.9ka. They provide a weighted mean of 92 ± 5ka for layers XVII to XXIII as a representative *terminus post quem* for the hominin sample, and note that when experimental errors are taken into account there are no systematic differences in age between the layers, suggesting that the deposits accumulated rapidly.

Schwarcz et al. (1988) provided ESR dates on bovid tooth enamel samples from the odd-numbered layers from XV to XXI, with an overall range using an early uptake (EU) model of 73.7ka to 119.0ka, and using a linear uptake (LU) model of 89.1ka to 145.0ka (no errors are given on the individual dates). The dates on layer XV, from which hominins 13 and 18 derive, are not significantly different from dates on the other layers; Schwarcz et al. (1988) thus provide weighted means for the whole sequence of 96 ± 13ka under EU-ESR and 115 ± 15ka under LU-ESR. Two of Scharcz et al.'s (1988) samples from layer XIX were re-dated by McDermott et al. (1993) using U-series methods, yielding dates of $88.61^{+3.24}_{-3.12}$ka on an enamel sample and $106.35^{+2.36}_{-2.31}$ka on a sample of dentine.

Yokoyama et al. (1997) provide direct U-series dates on the cranium of Qafzeh 6 using non-destructive gamma-ray spectrometry, with U-Th giving 80^{+24}_{-18}ka and U-Pa giving 94^{+10}_{-8}ka; these authors regard the latter age as more reliable, primarily due to its closer agreement with the findings of Valladas et al. (1988) and Schwarcz et al. (1988). Finally, a useful Bayesian stratigraphic model provided by Millard (2008) estimates an age of 87.0 – 95.2ka for the layer XVII hominins and 87.6 – 96.9ka for hominins 3 and 6. Given the lack of systematic age variance between layers and the arguments for rapid accumulation provided by Valladas et al. (1988) and Schwarcz et al. (1988), Millard (2008) further suggests that the layer XV hominins are likely to be of similar age to those from layer XVII. It should be noted, however, that only those ages from Valladas et al. (1988) are directly incorporated in Millard's (2008) model due to the lack of error margins in the Schwarcz et al. (1988) publication.

Figure 3 shows all published dates from Qafzeh, together with a band equivalent to Millard's (2008) Bayesian stratigraphic model encompassing hominins 3, 6, 8-12, and 14-17. Despite the fact that Millard's (2008) model is informed only by the dates from Valladas et al. (1988), and the caveat that there is considerable variation in the dates, it is clear that the other three empirical studies represented by the figure (Schwarcz et al. 1988; McDermott et al. 1993; Yokoyama et al. 1997) tend to support the bracket of c.87ka to c.97ka for the accumulation of the hominin material. This is particularly the case when EU-ESR dates are favoured over those produced via LU-ESR, which are in some cases considerably older. It can be asserted with relative confidence, therefore, that modern humans reached Qafzeh sometime within this 10ka date range.

3.3.2. Skhul

The site of Skhul, less than 50km from Qafzeh, was initially excavated by McCown as part of Garrod's Mount Carmel project between 1929 and 1935 (Garrod and Bate 1937; McCown and Keith 1939). There are three main stratigraphic layers (A-C), with the 10 hominins, most of which were intentionally buried (Stringer et al. 1989), occurring in layer B. Although layer B is internally divided into the softer sub-layer B1 and the harder B2, it is not clear from which of the sub-layers the hominins derive. Grün and colleagues (2005:329) note, however, that the burials of Skhul II, V, and XI come from increasingly harder sediments, while Garrod and Bate's (1937) diagrams show Skhul IX as buried close to the bedrock. Dates come from ESR on bovid teeth (Stringer et al. 1989; Grün et al. 2005), thermoluminescence on burnt flints (Mercier et al. 1993), and U-series analyses of faunal teeth and bones (McDermott et al 1993; Grün et al. 2005). Importantly, the study of Grün and colleagues (2005) also directly dated a molar from the Skhul II specimen and bone fragments from Skhul IX using a combined ESR and U-series approach.

The seven samples from two bovid teeth analysed by Stringer et al. (1989) yielded age ranges of 54.6 ± 10.3ka to 101.0 ± 19.0ka on the EU-ESR model and 77.2 ± 15.7ka to 119.0 ± 25.1ka on LU-ESR; these authors provide weighted means of 81 ± 15ka and 101 ± 12ka respectively. McDermott and colleagues (1993) dated the same teeth via U-series analysis, additionally providing dates on two rhinoceros teeth from layer B. While their U-series date for one of the teeth (Sample 521) is not dissimilar to that attained via EU-ESR at $80.27^{+0.55}_{-0.55}$ka, their other dates are much later, ranging from $40.43^{+0.21}_{-0.21}$ka to $45.53^{+0.74}_{-0.73}$ka. McDermott et al. (1993) note that these later dates could be indicative of post-depositional uranium uptake, but also raise the possibility, suggested initially by McCown (1937), that the Skhul hominins could fall into two chronologically distinct groups, with the sub-50ka dates indicate of the later group.

Some of the earliest dates for Skhul layer B are provided by the thermoluminescence analyses of Mercier et al. (1993) on burnt flints from the site. These range from 99.5 ± 15.9ka to 166.8 ± 26.8ka, with a weighted mean of 119 ± 18ka, and are thus considerably closer to the linear uptake dates of by Stringer et al. (1989) than those provided via the early uptake model. Indeed, the analyses of Grün et al. (2005) demonstrate the benefits of the former model, and accordingly LU dates alone are considered here. The combined LU-ESR / open system U-series weighted means provided by Grün et al. (2005) range from 66^{+16}_{-9}ka to 176^{+74}_{-34}ka, though the oldest dates are on a sample recovered from within 2 to 5cm of the bedrock.

Grün et al. (2005) again sampled the two teeth sampled by Stringer et al. (1989) and McDermott et al. (1993), yielding ages of 108^{+28}_{-17}ka and 94^{+19}_{-15}ka. Additionally, these authors dated a tooth from a bovid skull directly associated with Skhul IX and a tooth from a pig mandible found with Skhul V; these yielded ages of 147^{+36}_{-21}ka and 93^{+21}_{-12}ka respectively. Fragments of bone from Skhul IX provided a U-series age of 131 ± 2ka, but the authors regard this as potentially suspect (Grün et al. 2005:326). A molar from the Skhul II skeleton, however, gave a reliable age of 116^{+43}_{-24}ka. Summarising their results, Grün et al. (2005) consider two possible scenarios for the burials of Skhul II, V, and IX: firstly, that the three burials took place over a relatively short period of time within the interval 100ka to 135ka, and secondly that the more primitive Skhul IX was buried before the other two specimens, with a date for Skhul II and V given by the weighted mean of their two average US-ESR results at 98^{+19}_{-10}ka.

Figure 4 shows all published dates from Skhul, together with Grün et al.'s (2005) estimate for Skhul II and V. Also shown is Millard's (2008) Bayesian stratigraphic model for Skhul V, which gives an LU-ESR age bracket of 71-115ka. Millard (2008) also gives a bracket for Skhul IX of 106-173ka, and for all other hominins of 43-158ka. His analyses, however, cannot accommodate the combined U-series / ESR dates provided by Grün et al. (2005). The dates for Skhul are noticeably less constrained than those for Qafzeh, as the bounds on Millard's (2008) Bayesian modelling make abundantly clear. This may be due to the possibility that the Skhul burials do not represent one continuous phase of deposition, as noted by Grün et al. (2005). Importantly, however, both Millard's (2008) estimate for Skhul V and Grün et al.'s (2005) estimate for Skhul II and V overlap the period from c.87 to c.97ka that is the most likely age of deposition at Qafzeh. Furthermore, the age estimates for both sites accord well with recent genetic data on the initial dispersal of *Homo sapiens* out of Africa.

3.4. The genetics of Homo sapiens *dispersal*

Genetic studies have added considerably to the body of research on modern human origins, yet estimates of divergence and dispersal times are highly variable, and are fraught with methodological problems (Cox 2008; Endicott et al. 2009). The conclusion that the initial (successful) dispersal of modern humans out of Africa occurred at c.60ka is widely accepted, yet in a review of the relevant literature Boivin et al. (2013) found studies producing or employing estimates of between 85ka and 45ka. There are many potential reasons for such discrepancies, and together they highlight the uncertainties inherent in the use of 'genetic clock' methods for estimating divergence dates.

Potential sources of inaccuracy are briefly discussed here, and are highlighted by considering two recent estimates of the ‘Out of Africa II’ event (Scally and Durbin 2012; Fu et al. 2013). The overlap in these two estimates offers some hope of resolution, and suggests that the widely held assumption that Qafzeh and Skhul represent a ‘failed migration’ is by no means definitive.

Discrepancies in estimates of the *Homo sapiens* dispersal out of Africa (that is, the coalescence date of non-African populations) are caused by assumptions regarding the operation of the ‘molecular clock’, primarily the dating of the split used to calibrate the clock (normally the human-chimpanzee split) and the plausibility of constant mutation rates through evolutionary time, though the two methods by which the mutation rate itself is calculated also provide intriguing conflicts. The date of chimpanzee-human divergence is usually assumed to be c.6Ma, but putative fossil hominins close to or even pre-dating 6Ma (e.g. *Orrorin tugenensis* (Senut et al. 2001), *Sahelanthropus tchadensis* (Brunet et al. 2002)) cast doubt on this date, and molecular estimates themselves give ages between 4Ma and 8Ma (Bradley 2008). Calculated mutation rates produced via phylogenetic estimates (based on the proportion of differences between extant species and the ages of dated fossils ancestral to them) and pedigree-based estimates (per-generation calculations based on complete genomes of parents and their offspring) show considerable discrepancy, with the latter being considerably lower.

Perhaps most contentious, however, is the assumption that mutation rates have been constant through evolutionary time. The major problem in this case stems from use of the ρ averaging statistic, which has been shown by Cox (2008) to be considerably affected by population size and structure. Effective population sizes, as well as the effects of bottlenecks, founder effects, and reproductively divided populations all alter rate calculations, with Cox (2008) demonstrating that date estimates based on ρ have a downward (i.e. younger) bias, large asymmetric error variances, and a considerable risk of type I error. Many autosomal studies (e.g. Barreiro et al. 2005; Garrigan and Hammer 2006; Plagnol and Wall 2006) provide evidence supporting the intuitive notion that human populations were small and reproductively isolated during periods in human evolution preceding the Out of Africa I migration. The fossil evidence of considerable morphological variation in pene-contemporary early *Homo sapiens* populations surveyed above further supports this notion, as do morphometric studies of such variation. Gunz et al. (2009), for example, argue based on cranial morphometrics that early modern humans were already divided into different populations in Pleistocene Africa prior to dispersal. Evidence that mutation rates have slowed recently in the primates comes from Kim et al. (2006), suggesting that the assumption of constant mutation rates through evolutionary time is highly questionable.

Recently, estimates of pedigree-based whole genome mutation rates have been used to suggest a very different timescale for key events in human evolution, including the dispersal of *Homo sapiens* from Africa. Scally and Durbin (2012) rescale previous estimates provided using phylogenetically derived rates (typically in the region of 10^{-9} per base pair per year) with the pedigree-based rate estimate of $0.5\times10^{-9}bp^{-1}year^{-1}$ (i.e. half the phylogenetic rate estimate). This analysis yields nuclear genomic estimates of the split between the Yoruba and non-Africans (a proxy for the dispersal date) at between 90ka and 130ka, markedly older than the standard estimate of around 60ka. This date bracket does, however, correspond remarkably well to the bracket of 80-140ka provided by Keinan et al. (2007) for an early human bottleneck evident in single-nucleotide polymorphism data from the HapMap Project (Altshuler et al. 2005; Frazer et al. 2007). Keinan and collagues (2007; see also Wall et al. 2009) found evidence for two bottlenecks in this extensive dataset, neither of which encompasses the standard dispersal date of 60ka (the second bottleneck corresponds broadly to the LGM).

An interesting counterpoint to the above discussion, however, comes from results published by Fu et al. (2013), who argue via mtDNA sequences from ten radiocarbon dated prehistoric modern human specimens that the upper bound for the dispersal of *Homo sapiens* lies in the range between 62.4ka and 94.9ka (mean = 78.3ka). This finding would tend to revise the dispersal date back towards the traditional view, but note that the mean of 78.3ka is still substantially earlier than the figure of c.60ka, and pre-dates the Toba ‘super-eruption’, thought by a few researchers to be the cause of a substantial bottleneck *prior* to dispersal (e.g. Ambrose 1998; but see Petraglia et al. 2007). Although there are problems with the Fu et al. (2013) analysis – half the specimens come from just two sites (Dolni Vestonice and Oberkassel) – if it is cautiously interpreted it can be a useful addition to the debate. Although the authors admit (Fu et al. 2013:553) that mtDNA analyses tend to provide biased estimates of divergence dates, they correctly assert that such dates are statistically valid upper bounds. Thus a conservative use of Fu et al.’s (2013) findings would suggest that the dispersal of *Homo sapiens* out of Africa occurred *after 95ka*.

Putting the dispersal estimates of Scally and Durbin (2012) and Fu et al. (2013) together results in a period of overlap between the two estimates at 90-95ka. Given that the former paper uses a pedigree-based mutation rate estimate on whole genomes whilst the latter uses a phylogenetic mutation rate estimate on mtDNA data, it is gratifying that they overlap at all. More important, however, is the fact that this window of overlap is within Millard’s (2008) Bayesian stratigraphic estimate for the occupation of Qafzeh, and within both Millard’s (2008) and Grün et al.’s (2005) estimates for the occupation of Skhul. Whilst certainly not conclusive, this revised chronology, shown in Figure 5, forces us to admit the possibility that the inhabitants of Qafzeh and Skhul, and perhaps the postulated early *Homo sapiens* incursions into the Arabian peninsula (e.g. Armitage et al. 2011; Rose et al. 2011; Boivin et al. 2013) and ultimately India (Petraglia et al. 2007), were not 'failed dispersals', but played a role in the successful global diaspora of modern humans.

4. Climatic instability, plasticity, and dispersal

Section 2 demonstrated the pervasive effect of climatic variability in promoting plasticity, and further showed that successfully dispersing species are often those with a greater degree of plasticity. Section 3 detailed the evidence for the first appearance of *Homo sapiens* in Africa and its initial dispersal into the Levant at the sites of Skhul and Qafzeh. The current section introduces a model rooted in the biological theory of evolving plasticity, examines some basic results of that model using synthetic environments, and concludes by employing the model in conjunction with an empirical palaeoclimatic dataset directly relevant to the dispersal of *Homo sapiens* out of East Africa and into the Levant. Much research is now focused on the interaction between climatic change or variability and key events in human evolution such as patterns of speciation and extinction, the origin of our genus, the appearance of novel technologies, and the dispersal of hominin populations (e.g. Grove 2011a, 2011b, 2012a, 2012b; Potts 1998, 2013; Trauth et al. 2007, 2010). There is still much work to be done, however, on the precise nature of the relationships between climatic variables and trajectories of human evolution. In particular, more is needed on the distinction between the effects of variability and change (*sensu* Grove 2011b), and the analysis of specific, localized records directly relevant to the hominin populations under study.

The generic picture of the *Homo sapiens* dispersal into the Levant at c.90ka asserts that the climatic amelioration of MIS5 allowed the expansion of hominin populations out of Africa, following what is widely considered to be a bottleneck caused by the severe glacial conditions of MIS6. This is undoubtedly part of the story, but the increasing resolution and number of climatic records from East Africa between 200ka and the consolidation of the LSA should enable us to more closely examine potential drivers of expansion and dispersal, and to refine the picture of the particular trends in those records that correlate with the appearance of modern humans in regions from which they were previously absent. The following sections introduce a model that directly examines evolutionary trends through time in response to environmental data, validate that model with synthetic data, and finally implement it using a palaeoclimatic dataset from East Africa. The output of the model when used with such data allows for the formulation of predictions relating particular climatic trends to the evolution of plasticity and related dispersal capabilities.

4.1. A model of evolution under climatic instability

The model presented here is best described as a simple evolutionary algorithm (EA). It was designed to discover which kinds of climatic conditions lead to greater plasticity, and to simultaneously track the strength of directional selection and the fitness of the model population. Evolutionary algorithms first appeared in the computer science literature in the late 1950s and early 60s (see reviews by Bäck et al. 1991 and Mitchell 1996), and achieved something like their modern form with the work of Holland (1975). The work by Holland and colleagues on Genetic Algorithms (GAs; e.g. Holland 1975, 2000) contains some of the most widely known examples, but GAs are just one example of the use of evolution-like processes to solve complex problems. Since *in silico* evolution, like biological evolution, can rapidly search vast parameter spaces to find sets of successful solutions, EAs have found a substantial foothold as optimization algorithms in disciplines such as engineering. The model reported here, however, is somewhat closer in motivation to the original models of Holland (1975), in that is uses a computer programme to simulate and learn directly about the process of biological evolution.

Most EAs are designed to solve a static problem, or to find a single 'fittest' solution. The current model, by contrast, features a population that adapts to an environment which is itself constantly changing, and is thus a more direct analogue of biological evolution. The model features a fixed population size of 1000 individuals, with each individual having a single 'chromosome' encoding two values: the first value describes the environment to which the individual is the best suited, whilst the second is a measure of the individual's tolerance of surrounding environments. Mathematically, these two values are equivalent to the mean and standard deviation of a normal distribution which describes the individual's fitness over a proscribed range of environmental states (much like the curves produced in Figure 1). The two values for each individual are randomly seeded at the start of a simulation run by calling random variates from a normal distribution with a mean equivalent to the value of the environment in the first generation of the simulation and an arbitrarily small standard deviation of 0.25. Each generation a new environmental value occurs (it may be the same or different to the environmental value of the previous generation, depending upon the environment loaded into the program) and the fitness of each individual is evaluated. The fitness of an individual is the value of the normal probability density function given the environmental value and the mean and standard deviation of the individual.

Selection involves a simple ranking of individuals by fitness, with the 500 weakest individuals dying each generation, to be replaced by the offspring of a selection of the 500 fittest individuals. Individuals are selected as parents using Fitness-Proportionate Selection (FPS; see Mitchell 1996), whereby the probability of an individual being a parent, provided it is in the fittest half of the population, is directly proportional to its fitness. Since each individual has only two 'loci' on its chromosome, of the four possible offspring two will be clones of one of the parents (see Figure 6), with the other two being chromosomes potentially new to the population. Reproduction is thus one mechanism through which variation in the population is generated, with the second being mutation. Mutation is affected by the addition of a random variate, uniformly distributed on the interval (-0.005, 0.005), being added to each locus of each new offspring. The processes of selection, reproduction, and mutation are repeated each generation, in the relation to the environment experienced in that generation. A full illustration of model flow is given in Figure 7.

4.2. Basic model results

The model was first run on a series of synthetic environments designed to test responses to environmental change and variability. A final analysis tested the ability of populations adapted to varying levels of climatic variability to move successfully into different environmental regimes. Throughout, the averages of the mean, standard deviation, and fitness of the population are plotted and examined. In terms of the prior discussions, the standard deviation is regarded as being a measure of plasticity in the population. Key results are briefly summarised here; for a full, technical appreciation of the model, see Grove (2014).

4.2.1. Simple perturbation

The first analysis is designed to test the effects of a simple, directional change in climate on the model population. The environment consists of two simple shifts, from 1 to 1.5 in 0.01 unit per generation increments between generations 50 and 100, and similarly back to 1 between generations 550 and 600. The staging of these shifts is chosen to allow the population sufficient time to adapt to the first perturbation before initiating the second (with adaptation to the new environment considered complete when the mean of the output is equal to the value of the environment). The change from 1 to 1.5 (or vice versa) is slightly sloped rather than abrupt to allow the population to track it successfully. This reflects an immediate finding of the model: large, abrupt changes simply lead to 'extinction' due to the fact that, when there is not sufficient genotypic variation in the population, an abrupt change in environment leads to all existing genotypes having zero fitness. This finding is expanded upon below in relation to varying amplitudes of environmental variability.

Figure 8 shows the output of this model, with the environment plotted in Figure 8a. Figure 8b shows that the mean of the population rises sigmoidally to reach the new environmental value. As one would expect, there is a considerable lag in reaching this new value, and it is important to note that the population is only able to tolerate the change and continue to evolve towards the new environmental value due to rapid increases in the SD. Figure 8c demonstrates that as soon as the environment is perturbed, the SD begins to increase rapidly. The peak in plasticity corresponds to the point at which the mean is increasing most rapidly. Beyond this point the SD decreases again: such a wide tolerance is no longer needed as the mean approaches the optimum. Thus, a fundamental finding is that increases in the SD are a fundamental aspect of adaptation to the new environment. Finally, Figure 8d demonstrates that fitness declines abruptly when the environment is perturbed, as the population at the point of perturbation is well adapted to the prior environment. Though increasing values of the SD after perturbation do increase fitness (they would not be selected for otherwise), the most notable increases in fitness occur as the mean approaches the new environmental value and the SD declines. This finding requires a subtle deconstruction of causality: environmental change causes reduced fitness, and also causes increases in the SD; although high SD values are associated throughout with relatively low fitness, they in fact cause an *increase* in fitness relative to fitness levels the population would have achieved without increased SD values.

4.2.2. Changing amplitudes of environmental variability

The environment in this second analysis is a simple sine wave of period (500/23)≈ 21.74 generations. It has an amplitude of 0.4 from generations 1-500 and 1001-1500, and an amplitude of 2 from generations 501-1000. The changes in amplitude are marked as 1 and 2 in Figure 9, with Figure 9a showing the environment.

Figure 9b shows that the mean asymptotes and remains throughout at a value close to 0, the mean of the environmental oscillation. It also maintains an oscillation in period equivalent to that of the sine wave, but at a much lower amplitude of ≈ 0.02. That the amplitude of the mean is much lower than that of the environment is due to the buffering effects of the SD. Figure 9c shows that the SD quickly settles to a level sufficient to minimize the effects of environmental fluctuation on the population in generations 1-500 (prior to Line 1 in Figure 9). It also maintains an oscillation with a period half that of the environment, but again at a low amplitude of ≈0.02 throughout (the period is half that of the environment because it is the magnitude of the *absolute* difference between the mean and the environment that governs selection on the SD). After Line 1, as the amplitude of environmental change increases, the SD increases with it, though there is again an inevitable lag. After Line 2, as the amplitude of environmental change decreases, so the SD also decreases. The critical finding here is that increases in the amplitude of environmental *variability* lead to increases in the SD. This is in line with much of the work by Potts (1998, 2013) and Grove (2011a, 2011b) on the effects of environmental variability. However, note from Section 4.2.1. that directional environmental *change* also leads to increases in the SD; the primary difference is that change increases the SD as a short-term buffer, whereas variability maintains a consistently high SD equivalent to a standing level of plasticity in the population.

Figure 9d (grey line) shows that fitness oscillates at high amplitude relative to the environment, and is generally higher in generations 1-500 and 1001-1500 (i.e. prior to Line 1 and after Line 2, when the environment is varying at lower amplitude). The black line in Figure 9d gives an exponentially smoothed fitness trajectory which is more useful for interpretation. In terms of the capacity for dispersal, the most important area of Figure 9d is that covering the ~100 generations following Line 2, when environmental variability is at low amplitude but the SD remains high. This combination leads to very low variance in fitness, noted in Section 2 as critical for survival under climatic instability. It is during this period, when the SD remains at a level greater than that required by the environment, when the population is best equipped to disperse into neighbouring regions. High levels of the SD equip the population to deal with a greater range of environments than the range they are actually experiencing in situ.

4.2.3. Standing plasticity and the response to relocation

The final analysis performed with the model using synthetic data involves two populations. Initially, the two populations face separate environments with equal means of zero but different levels of environmental variability (one at an amplitude of 2.0, the other at an amplitude of 0.4). The variability is slowly increased over the first 500 generations in both cases. After 1000 generations, both populations are transferred to a new environment with a mean of 1 and an amplitude of 0.4. The environments experienced by both populations are plotted in Figure 10a. It should be noted that the two populations are not strictly competing in the latter environment; rather, the model is run as though there is ample space for both, and examines how long it takes each to acclimatise.

Figure 10b shows that during the first 1000 generations the means of the two populations are very similar, despite the marked difference in environmental variability. This is because both environments have means of 0, and the greater variability in Environment 2 (blue) is accommodated via higher SD values in Population 2. After the switch to the second environment after 1000 generations (purple line, experienced by both populations), Population 2 (blue) approaches the new environmental mean of 1 at a faster rate. Figure 10c demonstrates that, as expected following the results of Section 4.2.2., the population experiencing higher environmental variability (Population 2) develops a markedly higher SD than the low-variability population. After 1000 generations, the SDs of both populations increase further, but for Population 2 it is a short-lived increase, after which the SD declines steadily to reach the level shown during the first 1000 generations by Population 1. The SD of Population 1 after 1000 generations increases rapidly, peaking after 1340 generations and thereafter declining to a level similar to that of the first 1000 generations.

The fitness of the two populations, graphed in Figures 10d and 10e, shows some interesting features that are informative about the abilities of populations witnessing different levels of environmental variability to colonise new environments. For the first 1000 generations, fitness is higher in Population 1 simply because it experiences a less variable environment. In the second 1000 generations, however, after displacement to the new environment, the fitness of Population 2 is consistently higher (this is considerably clearer in the inset Figure 10e). This is because the greater SDs of Population 2 provide more variation in fitness for selection to act upon. The existence of such variation allows selection to pull the mean more quickly towards the new environmental value. The crucial finding here, therefore, is that populations experiencing greater levels of environmental variability will be more capable of successfully colonising new environments due to their elevated levels of plasticity. This finding is directly in line with the thinking of evolutionary theorists such as Mayr (1965) and Baker (1965). Environmental variability is key in retaining higher levels of plasticity, as in static environments selection will quickly reduce plasticity to increase fitness. In Holland's (1975) terms, a population experiencing a relatively constant environment will become 'over-adapted' to that environment, and will thus be incapable of adapting to environmental change.

4.3. Expectations regarding dispersal

Sections 4.2.1. and 4.2.2. show the basic responses of the model to climatic change and variability, and section 4.2.3. gives an impression of the value of plasticity in a relocation scenario. Putting these findings together, we can begin to formulate a series of expectations about the environmental conditions that favour dispersal; we can then search for these conditions in empirical palaeoclimate curves to find chronological intervals during which dispersal would have been particularly likely. Grove et al. (submitted) put forward a simple dispersal hypothesis based on the facts that a) temporal variability in the environment can lead to the evolution of plasticity and b) successful dispersers tend to be highly plastic relative to unsuccessful sister taxa. They suggest that dispersal is most likely in stable periods immediately following periods of high climatic variability. In such stable periods, plasticity accumulated during conditions of high environmental variability is expressed in dispersal; animals are tolerant of a wider range of conditions than those they experience in their natal environments, and are thus equipped for dispersal into neighbouring regions. The modelling detailed above supports this hypothesis in generic terms, but also allows for the formulation of some more precise expectations in terms of plasticity and fitness. Animals are particularly well equipped for dispersal when:

1. Relatively stable climatic periods immediately follow periods of high climatic variability.

This situation has a number of recurrent correlates in the model:

2. The SD is relatively high but declining. And;
3. Fitness is relatively low but increasing.

(3) also entails the further correlate that population size is increasing, but since this is not explicitly tested here, confirmation is left to future work. The empirical record below, therefore, is examined for the timing of the above indicators.

4.4. Running the model with palaeoclimatic data

As the focus of the current contribution is the early dispersal of *Homo sapiens* populations out of East Africa and into the Levant, a palaeoclimatic dataset from Ethiopia – the most likely origin point of modern humans – was chosen as the empirical record on which to run the model. The preceding analyses give a flavour of the basic results to be expected from simple, synthetic environments, but the analyses reported in the current section allow for the derivation of predictions about the timing of dispersal. The empirical record is simply substituted for the synthetic records thus far used, with run length adjusted accordingly. The value of implementing the model in this way is that it allows us to search the output for the occurrence and timing of any of the indicators indentified above as likely correlates of or stimuli towards dispersal.

Lake Tana is situated on the basaltic plateau of northwest Ethiopia, at 12°N, 37°15’E (see Marshall et al. 2011 for a full geological description). It is fed by four permanent rivers, and forms the source of the Blue Nile. Extensive work on palaeoenvironmental proxies covering the last 250ka from Lake Tana cores has been carried out by Lamb and colleagues (submitted), and this work should be consulted for full descriptions of proxy data analysis and age modelling. A relatively continuous section of data from the Lake Tana cores comprising the calcium / titanium ratio as a precipitation proxy (see, for example, Jaeschke et al. 2007) between 80ka and 150ka is used as the environmental input to the model in this case. Although proxy values recovered from the core over this period average slightly more than one per twenty year interval, they are unevenly spaced in time; since the model requires evenly spaced chronological intervals, linear interpolation was used to derive one value per generation (one generation = 20 years).

Figure 11 shows the output of the model when run on the Lake Tana precipitation proxy from 150ka to 80ka (note that, unlike previous figures, Figure 11 should be 'read' from right to left; that is, the run starts at 150ka and ends at 80ka). Figure 11a shows the output mean overlaid on the actual data, and demonstrates that moisture levels fluctuate far too rapidly for the population (as modelled) to effectively track them via directional selection. The recombination and mutation rates used in the model are high relative to those of modern humans, though of course recombination in a diploid organism with 46 chromosomes would lead to the generation of substantially more variation than occurs in the haploid, two-locus model used here. The relative scaling of these parameters is, however, of limited importance in the interpretation of the output presented here, as it has only linear effects on the results (see Grove 2014). Decreasing the mutation rate, for example, further smoothes the curve of the mean shown in Figure 11a, increasing the distance between it and the actual climate curve throughout the run; it does not, however, change the position or the relative heights of the peaks in the SD or fitness output. This leads to a reassuring homogeneity of resulting SD and fitness output between runs.

Figure 11b provides an interesting example of how both climatic *variability* and climatic *change* can lead to increases in plasticity although, as per the experiments with the synthetic environments reported above, only high variability has the potential to lead to the long-term maintenance of high levels of plasticity. The Tana record shows high levels of variability between c.138ka and c.120ka (Figure 11a, grey line), with accordingly high values of the SD over the same period (Figure 11b). However, a major directional change in the Tana record at ~113ka also leads to a substantial increase in the SD, peaking approximately 4ka later, and then quickly declining again to a very low level by ~103ka. It is at the end of this decline that the first potential dispersal pulse occurs, with the coincidence of a phase of environmental stability with a high but decreasing level of plasticity and rapidly increasing fitness (Figure 11c). Similar phases occur from c.102-100ka and c.99-97ka, though on the low variability criterion alone we might consider these three events to be part of a single phase (see Figure 11). Aside from possible small pulse around 116ka, the phase comprising these three events is the only viable dispersal interval between 80ka and 145ka evinced in the Lake Tana data. This suggests that a significant dispersal event from East Africa could have occurred in the period c.105-97ka.

Returning to the Levantine data presented in Figures 3 and 4, Qafzeh is most likely to have been inhabited sometime between c.87ka and c.97ka, with a somewhat less constrained date for Skhul V of c.71-115ka (Millard 2008) or, using Grün et al.'s (2005) US-ESR estimate for Skhul II and V, c.88-117ka. These dates are consistent with the finding of a dispersal event originating in Ethiopia (or a nearby region with a synchronous climate) occurring between c.97. and c.105ka. As summarised in Figure 5, there is a notable coincidence between the most likely dates for Qafzeh and Skhul and recent genetic dates for the start of *Homo sapiens* dispersal out of Africa. These two genetic studies (Scally and Durbin 2012; Fu et al. 2013), despite employing different methods and utilizing different mutation rate estimates, nonetheless achieved a region of overlap between 90ka and 95ka, which further overlaps with the dates for the occupation of Qafzeh and Skhul.

A combination of the analyses presented here with recently published fossil and genetic data, as synthesized in Section 3 (above), suggests that *Homo sapiens* achieved morphological modernity in East Africa sometime after 200ka, though possibly as late as 150ka. These early African modern humans, however, were relatively constricted in terms of population sizes and geographical ranges due to the severe climate of MIS6. The mosaic morphology of so many of the pseudo-modern crania reported in Section 3 suggests that elements of modern morphology appeared piecemeal, probably in reproductively isolated populations separated by uninhabitable tracts of cold, arid terrain. The modelling reported above suggests a pulse or pulses of dispersal from Ethiopia (and climatically synchronous areas of East Africa) between c.97 and 105ka, and the estimates of Grün et al. (2005) and Millard (2008) suggest modern humans reached Qafzeh between c.87 and 97ka, with Skhul dated to a wider bracket around a similar mean. Crucially, the new genetic dates force us to admit the possibility of a Levantine modern human population c.90-95ka forming not a ‘failed dispersal’, but part of the successful global diaspora of modern humans.

Doubtless the possibility that Skhul and Qafzeh are waypoints on a successful path of global dispersal will remain a minority view, but it is useful at this stage to pick apart the plausibility of the dates identified in the Lake Tana record as the start of a dispersal event (globally successful or not) that led to the initial colonisation of the Levant by modern humans. By taking the dates of the Lake Tana dispersal phase (105-97ka) and the most likely Levantine occupation phase (97-87ka), together with an informed estimate of the distance from Ethiopia to the Levant of 4,000km, we arrive at dispersal speeds of ≥0.22km/year, with a mean of 0.44km/year. These figures in fact seem remarkably low; a population expanding by a distance a little more than a lap of the athletics track each year could easily have dispersed from Ethiopia to the Levant in the timescale suggested by the above analyses. Diffusion coefficients are notoriously difficult to estimate, especially for extinct taxa, but an indicative comparison comes from Anton et al. (2002), who estimated the dispersal speed of *Homo erectus* from Africa to Indonesia at 0.1 to 2.19km/year (these figures are the square roots of their area/year estimates).

The geographical position of Ethiopia also admits two possible, approximately equidistant routes to the Levant: an African route through the Sudan and Egypt along the west coast of the Red Sea, or an Arabian alternative through Yemen and Saudi Arabia, to the east of the Red Sea. Much discussion of the viability of a Bab al Mandab sea crossing has focused on the plausibility of rapid dispersal along the southern coast of present day Yemen and Oman, with implications for the colonisation of southern Iran, Pakistan, and India (Petraglia et al. 2007; Armitage et al. 2011; Rose et al. 2011). Crossing the Bab al Mandab straits could, however, have been equally important in providing an alternative route north towards the Mediterranean. Sea level and shoreline reconstructions for the Red Sea by Lambeck and colleagues (2011) suggest that at c.96ka the distance across the Bab al Mandab straits would have been <5km, with the Arabian shoreline clearly visible from Africa.

Abundant Middle Palaeolithic surface finds in Arabia attest to a considerable human presence (Groucutt and Petraglia 2012), but fossil hominins remain absent and dates are scarce. The date of Jebel Faya (UAE; Armitage et al. 2011) at c.125ka is remarkably early for a site so far east (it is over 3,000km from the Bab al Manbab straits assuming a route along the southern coast), but the Omani complexes studied by Rose and colleagues (2011) fit the Lake Tana dispersal chronology extremely well. Aybut al Auwal, dated by OSL to 106±9ka, and with purported Nubian affinities (Rose et al. 2011), is just over 2,000km from the Bab al Mandab; if the true date is 100ka, this would imply dispersal speeds from Ethiopia of 0.4km/year, similar to those cited above for dispersal northwards to the Levant. The data are consistent, therefore, with a dispersal of *Homo sapiens* northwards either within Africa or within Arabia; on the latter explanation, a founding southern Arabian population could have split to reach Oman by c.100ka and the Levant by around five thousand years later.

5. Summary and Conclusions

This contribution has surveyed the biological evidence for the evolution of plasticity and examined the fossil and genetic chronologies of the origin and initial dispersal of *Homo sapiens* into the Levant against the backdrop of this evidence. A model of the evolution of plasticity that can be run on palaeoclimatic datasets has been formulated, and initial results of that model using data from Lake Tana fit well both with theories concerning the relationship of plasticity to dispersal in general and with the modern human chronology detailed here. The key theoretical tenets, surveyed in Section 2 and confirmed by the model of Section 4, are that temporal variability in environments is likely to lead to the evolution of plasticity and that such plasticity is characteristic of successfully dispersing species.

The chronology of *Homo sapiens* dispersal is undoubtedly more complex than was once imagined. Modern humans arose in East Africa sometime after 200ka, but the mosaics of archaic and modern human features characterising almost all candidates for the first members of our species suggest that, prior to dispersal, populations were already small, reproductively separated, and approaching our definitions of anatomical modernity via several spatio-temporally distinct morphs. The severe climates of MIS6 are doubtless at least partly responsible for the apparently disparate nature of human occupation during this period, and the warmer conditions of MIS5, whilst providing more amenable circumstances for population increase and dispersal, interacted with more specific evolutionary dynamics favouring expansion. The first modern humans outside Africa appear in the Levant shortly after 100ka, and this first dispersal has, despite considerable study, remained an enigmatic event.

Section 4 brings together the previous sections of the paper via a model of evolving plasticity. When used on synthetic environmental datasets this model confirms many of the findings reported in Section 2, including the largely neglected fact that species showing higher levels of plasticity are more capable of successful dispersal. However, it also advances our understanding of the environmental correlates of plasticity by registering the different effects of climatic change and climatic variability (*sensu* Grove 2011b). Of particular importance is the finding that, whilst climatic change can lead to elevated levels of plasticity in the short term, climatic variability maintains consistently high levels of plasticity. Three related signals of the capability for dispersal are identified via these synthetic datasets, and can thus be sought as indicators of such capabilities in empirical records. Relatively stable conditions immediately following periods of relatively high climatic variability are found to be conducive to dispersal; in such periods, plasticity is high but decreasing, and fitness is low but increasing. It should be noted that, in the terms of the model, these are not three separate indicators, but rather three facets of a single complex that equips species for dispersal.

When the model is run using data from Lake Tana this complex occurs in a very obvious three-pulsed dispersal phase between c.105ka and c.97ka, during the most stable climatic period evidenced in the cores. Even relatively slow dispersal speeds would allow hominins dispersing from the Lake Tana area during this phase to reach Qafzeh and Skhul during their most likely dates of occupation. Of further interest is the fact that certain dates from sites on the postulated southern route out of Africa and through Arabia also fit this chronology remarkably well. Recent genetic data add a further coda: though widely regarded as a ‘failed’ dispersal, the current most likely dates for the coalescence of non-African *Homo sapiens* populations admit the possibility that Qafzeh, Skhul, and the complex of sites around Aybut al Auwal were in fact part of the successful global diaspora of our species.

Future work should continue to focus on the specific, localised dynamics of the relationship between climatic change and human evolution. Such work must be informed by a proper understanding of the relevant tenets of evolutionary theory as well as detailed study of the fossil, archaeological, and genetic material. Quantitative models are invaluable in the formulation and grounding of hypotheses, and the explicit coupling of such models with high resolution palaeoclimatic data provides a highly promising and currently under-exploited avenue of research. Models such as that formulated above allow us to combine an extensive body of well-established biological theory with directly relevant palaeoclimatic data, and thus to arrive at a far more robust and complete understanding of human evolution than has hitherto been possible.

Acknowledgements

I am very grateful to Henry Lamb, Helen Roberts, Sarah Davies, Mike Marshall, Richard Bates and Dei Huws for making the Lake Tana data available to me. I would also like to thank Christine Ogola, Stephen Rucina, and the Organising Committee who made the 2013 EAQUA 4th Workshop in Nanyuki, Kenya, such a stimulating meeting to attend. Finally, I would like to thank John Gowlett for facilitating my time in Kenya and for encouraging me to participate in the Nanyuki Workshop.

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Table Caption

Table 1. Parameters of the four populations plotted in Figure 1 and their fitnesses in differing environmental states. In a spatially heterogeneous environment Population 2 dominates due to its higher arithmetic mean; in a temporally heterogeneous environment, however, Population 4 dominates due to its higher geometric mean.

Figure Captions

Figure 1. The fitnesses of the four populations in differing environment states. A) shows the fitness distributions of the four populations, B) the temporally heterogeneous environment they are subject to, and C) a standard single-locus population genetic outcome of selection under the environment shown in B).

Figure 2. Output of the Moran (1992) model under spatially (A, C) and temporally (B, D) heterogeneous environments. A and B show the basic output (after Moran 1992), with C and D showing how the parameter space is partitioned among the various strategies.

Figure 3. Radiometric dates for early *Homo sapiens* levels at the site of Qafzeh, Israel. Diamonds are electron spin resonance (ESR) dates from Schwarcz *et al*. (1988), with black indicating early uptake (EU) and white indicating linear uptake (LU) models; squares are thermoluminescence dates from Valladas *et al*. (1988); triangles are ESR dates from McDermott *et al*. (1993), with EU-ESR and LU-ESR indicated as before; open circles are uranium series dates from McDermott *et al*. (1993); black circles are U-series dates on the Qafzeh 6 cranium from Yokoyama *et al*. (1997). Error bars are shown where the relevant data were published. The grey region 87.0-96.9ka BP is that indicated by Millard's (2008) Bayesian stratigraphic model as encompassing the layers from which hominins 3, 6, 8-12, and 14-17 were recovered.

Figure 4. Radiometric dates for early *Homo sapiens* levels at the site of Skhul, Israel. Diamonds are combined open-system U-series and linear uptake ESR (henceforth US-ESR) dates from Grün *et al*. (2005), with grey indicating individual dates and black indicating weighted means for each sample (confidence intervals are shown for the means only); squares are from McDermott *et al*. (1993), with white being LU-ESR and black being U-series dates (note that the confidence intervals on the U-series dates are shown, but are negligible at this scale); triangles are LU-ESR dates from Stringer *et al*. (1989); circles are TL dates on burnt flint from Mercier *et al*. (1993). The light grey regions are those indicated by indicated by Millard's (2008) LU-ESR Bayesian stratigraphic model for the burial of Skhul V (associated with sample 1058) and Grün *et al*.'s (2005) combined US-ESR analysis for the burials of Skhul II and V. The darker grey region is the period of overlap in these two estimates from 88 – 115ka BP.

Figure 5. A combined plot of the date estimates from Millard (2008) for Skhul and Qafzeh and Grün *et al*. (2005) for Skhul (see Figures 3 and 4) with recent genetic estimates of the date of *Homo sapiens* dispersal out of Africa from Scally and Durbin (2012) and Fu *et al*. (2013). The vertical dashed lines indicate the period, c.90-95ka, during which all five date ranges overlap.

Figure 6. The production of new offspring via recombination in the evolutionary algorithm. Two parents, each of which have two loci, can produce four distinct offspring types, of which two are

clones of one or other parent. Arrows indicate input of parental values to offspring; grey borders indicate the pathways of clonal reproduction.

Figure 7. Process diagram of the evolutionary algorithm. The fitness function assigns a fitness score, $f(i,g)$, to an individual i in generation g according to the normal probability density function given the mean, μ_i, and the standard deviation, σ_i, of that individual and the value, e_g, of the environment in that generation, $f\left(i,g\middle|\mu_i,\sigma_i,e_g\right)=\frac{1}{\sigma_i\sqrt{2\pi}}\exp^{\frac{-\left(e_g-\mu_i\right)^2}{2\sigma_i^2}}$. j is calculated by rounding 500 uniformly distributed pseudorandom numbers on the open interval (0,1) to the nearest integer and summing the resulting vector. This is equivalent to a normal distribution with $\mu=250$ and $\sigma^2=125$. It is recalculated each generation. k is calculated as $k=500-j$, thus across generations $\bar{j}=\bar{k}=250$. FPS stands for Fitness-Proportionate Selection throughout.

Figure 8. Results of the evolutionary algorithm when the population is subject to simple perturbations, showing a) the environmental regime, b) the response of the mean, c) the response of the standard deviation, and d) the fitness of the population as raw output (grey) and an exponentially smoothed trajectory (black).

Figure 9. Results of the evolutionary algorithm when the population is subject to varying amplitudes of environmental variability, showing a) the environmental regime, b) the response of the mean, c) the response of the standard deviation, and d) the fitness of the population.

Figure 10. Results of the evolutionary algorithm on two populations evolving under different levels of environmental variability. For the first 1000 generations, Population 1 (blue line) evolves under conditions of greater environmental variability than Population 2 (red line). For the second 1000 generations, both populations are relocated to a new environment with a higher mean and a low environmental variability (shown by the purple line in a)). a) shows the environmental regimes, b) the response of the means, c) the response of the standard deviations, and d) the fitnesses of the two populations as raw output (lighter shades) and exponentially smoothed trajectories (darker shades). The inset e) magnifies the section of d) showing the fitnesses of the two populations over the second 1000 generations.

Figure 11. Results of the evolutionary algorithm run on the Lake Tana data. a) shows the Ca/Ti moisture proxy from Lake Tana, with the response of the mean overlaid, b) shows the response of the standard deviation, and c) shows the fitness of the population. The identified dispersal phase is shown in light amber, with the three numbered darker bars indicating the three identified pulses of dispersal within that phase.

Tables

Table 1

	Parameters		Environmental State			Means	
Population	**Mean**	**SD**	**3**	**5**	**7**	**Arithmetic**	**Geometric**
1	3	0.8	0.499	0.022	0.000	0.174	0.003
2	5	0.8	0.022	0.499	0.022	**0.181**	0.062
3	7	0.8	0.000	0.022	0.499	0.174	0.003
4	5	1.3	0.094	0.307	0.094	0.165	**0.139**

Figures

Figure 1

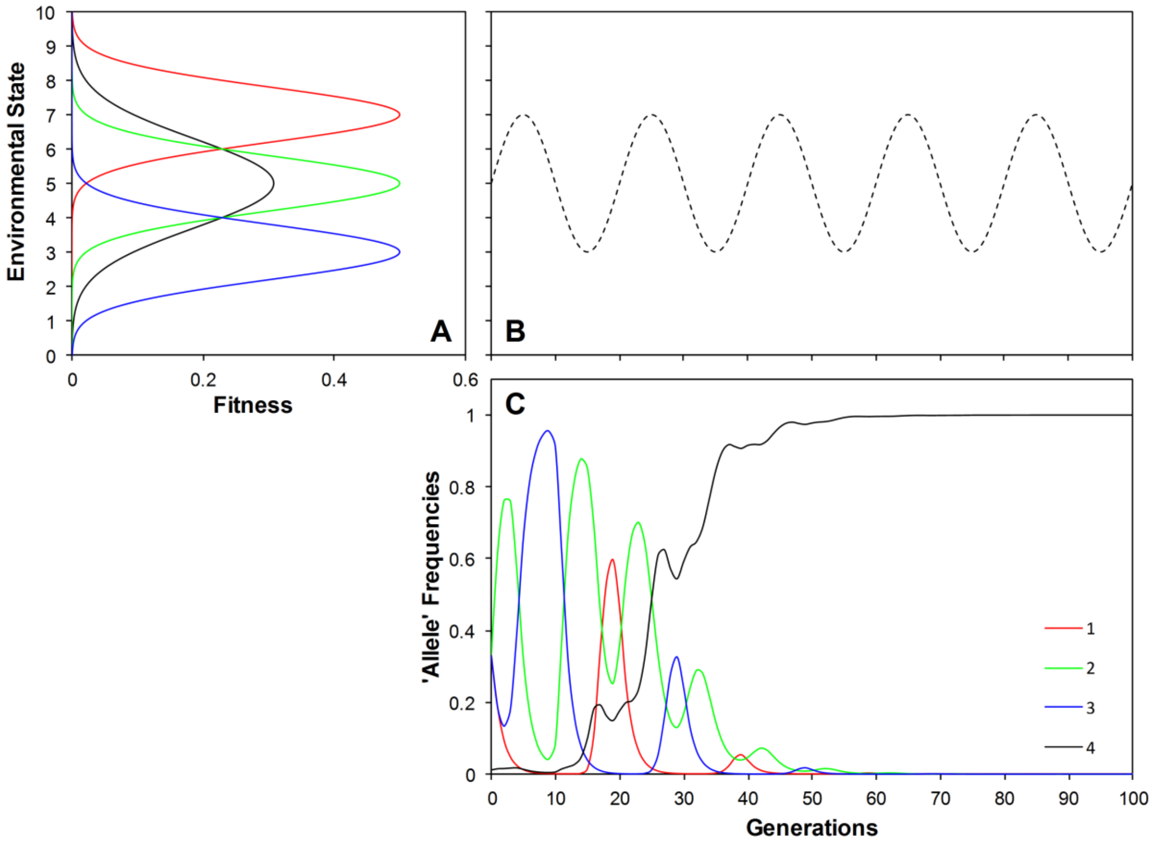


Figure 2

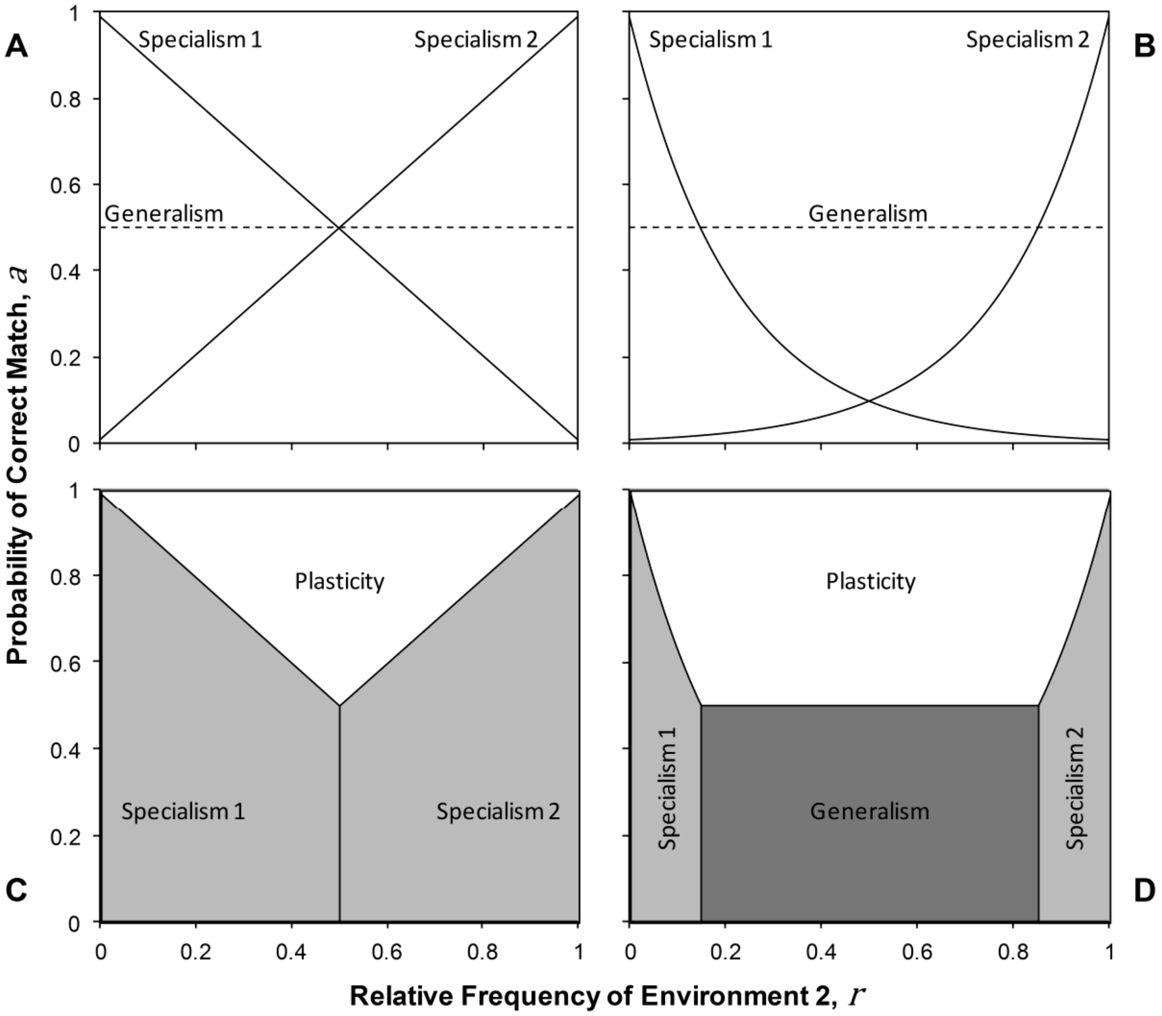
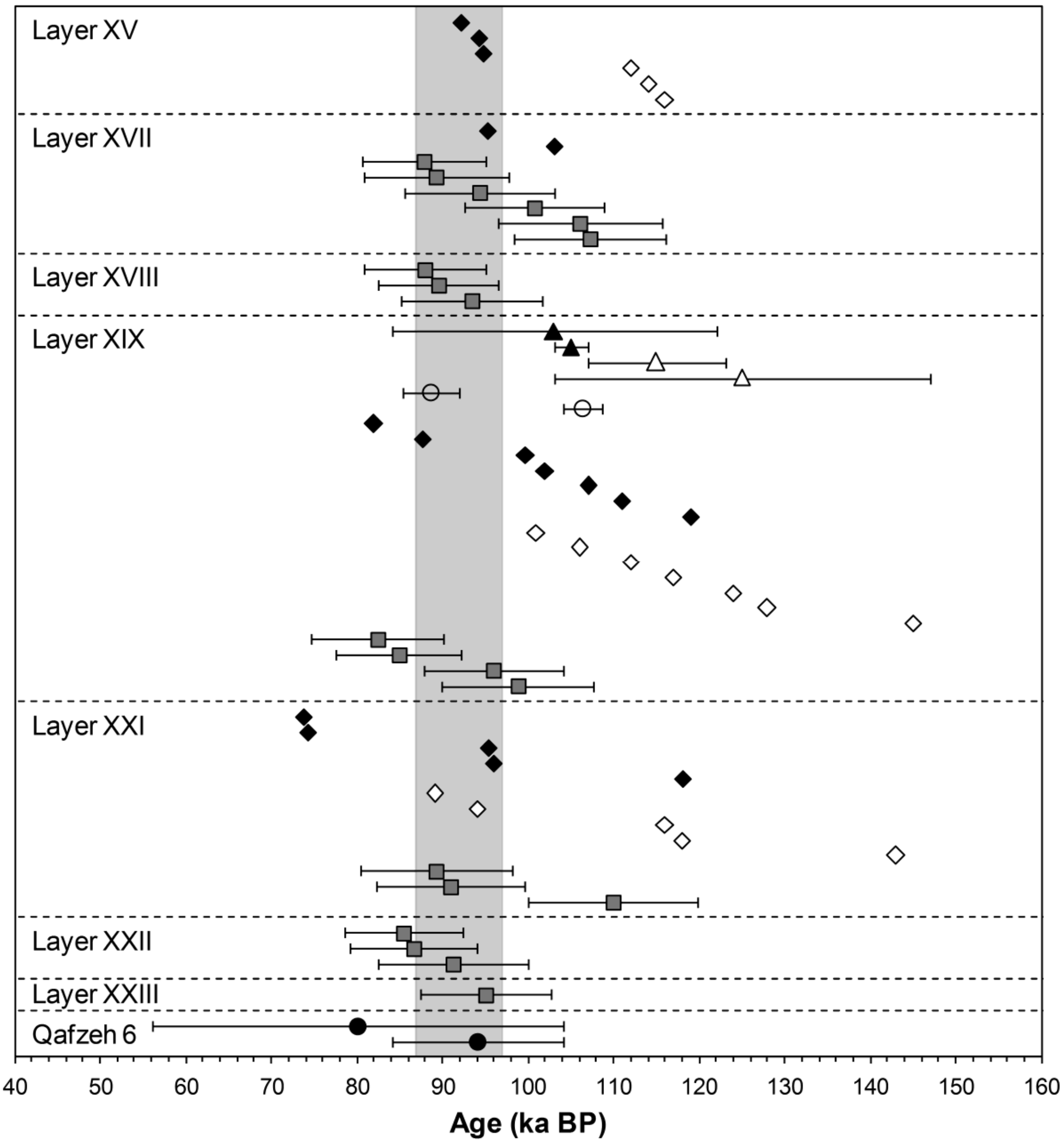

A
B
C
D
Specialism 1
Specialism 2
Generalism
Plasticity
Probability of Correct Match, a
Relative Frequency of Environment 2, r
0
0.2
0.4
0.6
0.8
1

Figure 3



Layer XV
Layer XVII
Layer XVIII
Layer XIX
Layer XXI
Layer XXII
Layer XXIII
Qafzeh 6
40
50
60
70
80
90
100
110
120
130
140
150
160
Age (ka BP)

Figure 4

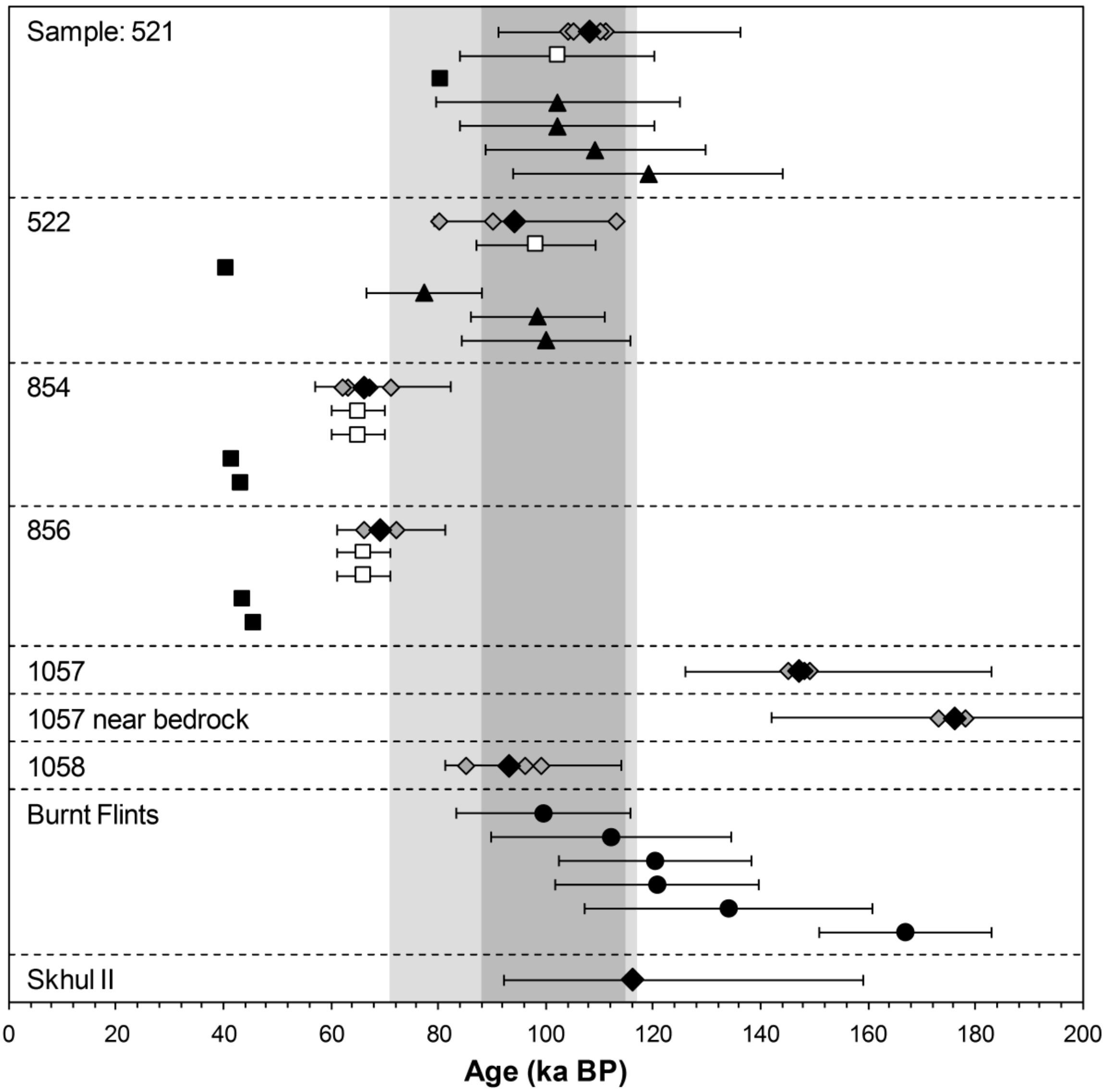

Sample: 521
522
854
856
1057
1057 near bedrock
1058
Burnt Flints
Skhul II
0
20
40
60
80
100
120
140
160
180
200
Age (ka BP)

Figure 5

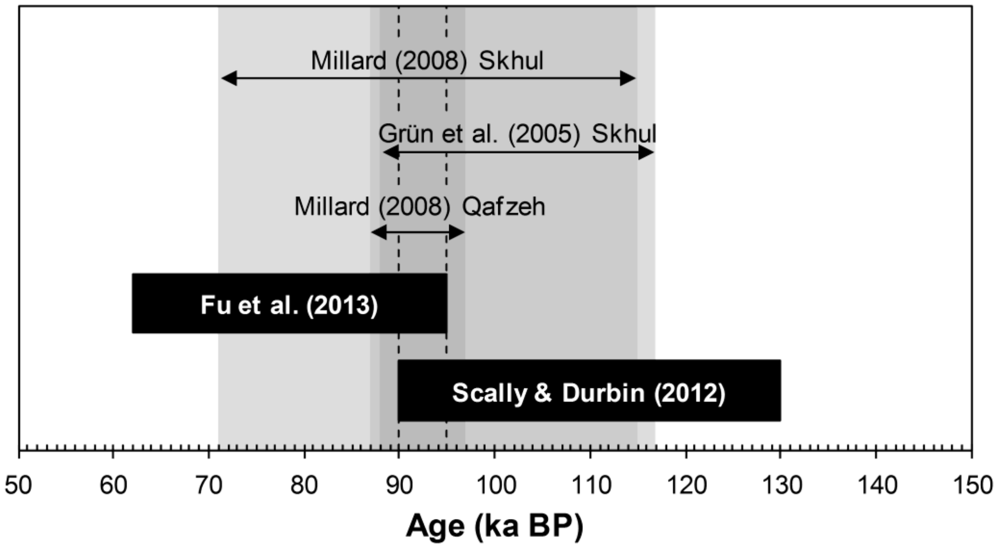

Millard (2008) Skhul
Grün et al. (2005) Skhul
Millard (2008) Qafzeh
Fu et al. (2013)
Scally & Durbin (2012)
50
60
70
80
90
100
110
120
130
140
150
Age (ka BP)

Figure 6

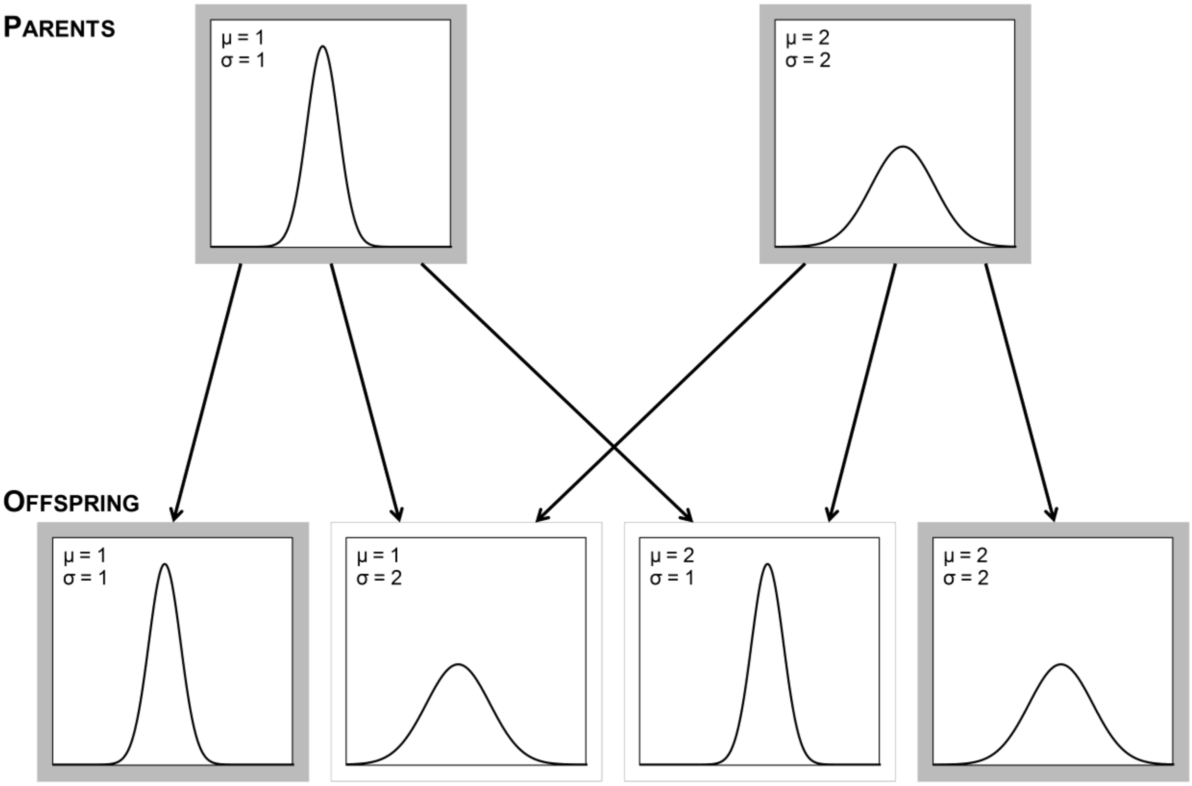


Figure 7

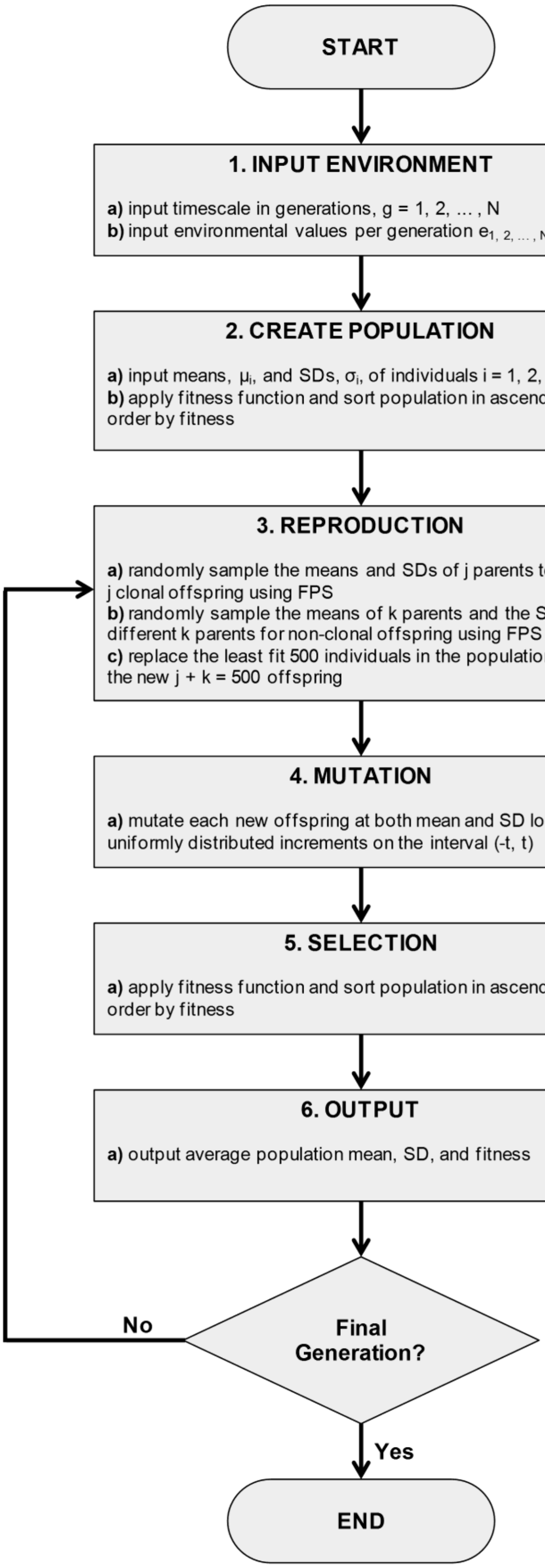

START
1. INPUT ENVIRONMENT
a) input timescale in generations, g = 1, 2, … , N
b) input environmental values per generation e1, 2, … , N
2. CREATE POPULATION
a) input means, μi, and SDs, σi, of individuals i = 1, 2, … , M
b) apply fitness function and sort population in ascending order by fitness
3. REPRODUCTION
a) randomly sample the means and SDs of j parents to create j clonal offspring using FPS
b) randomly sample the means of k parents and the SDs of a different k parents for non-clonal offspring using FPS
c) replace the least fit 500 individuals in the population with the new j + k = 500 offspring
4. MUTATION
a) mutate each new offspring at both mean and SD loci by uniformly distributed increments on the interval (-t, t)
5. SELECTION
a) apply fitness function and sort population in ascending order by fitness
6. OUTPUT
a) output average population mean, SD, and fitness
Final Generation?
No
Yes
END

Figure 8

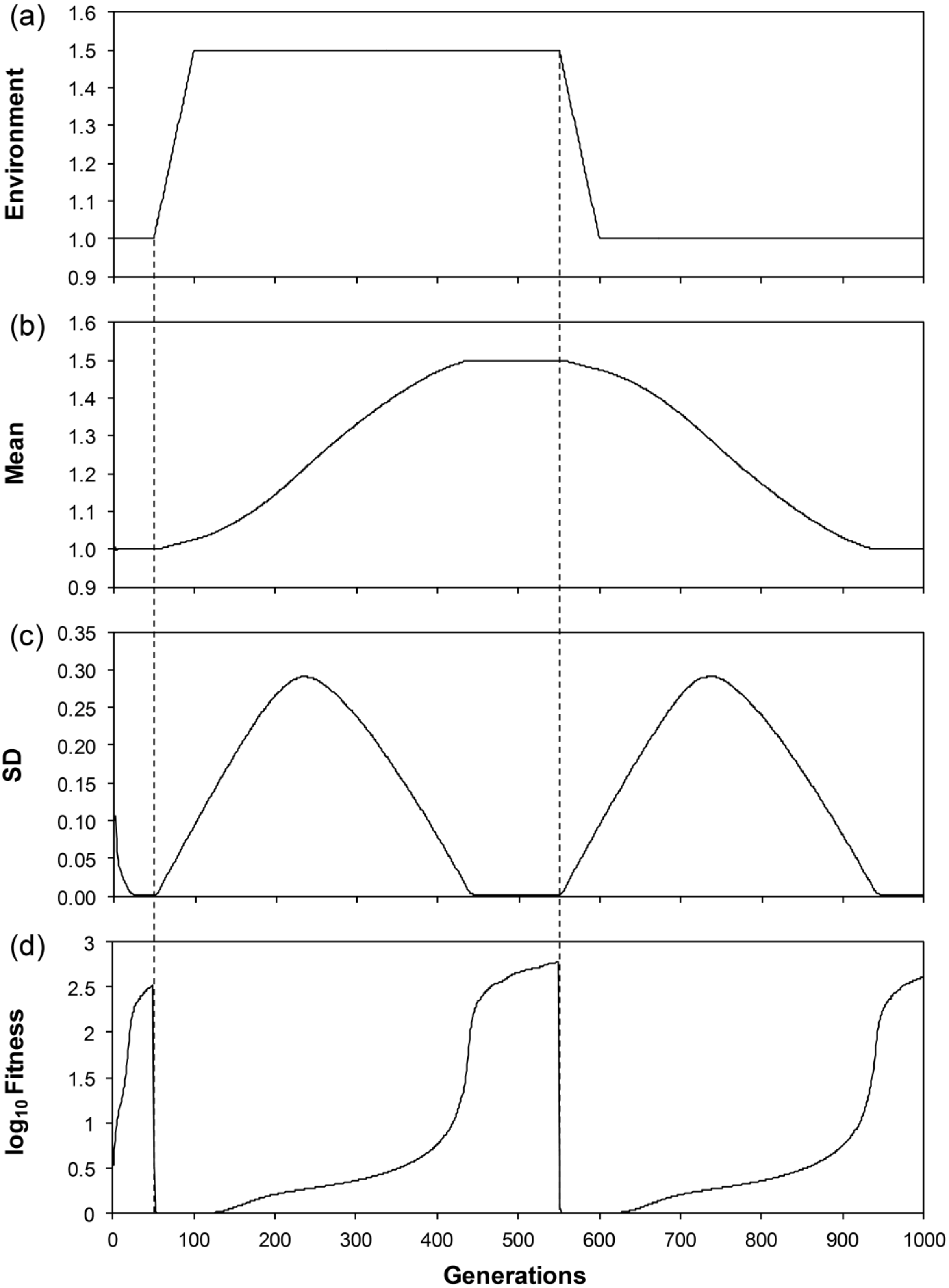

(a)
Environment
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
(b)
Mean
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
(c)
SD
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
(d)
log10 Fitness
3
2.5
2
1.5
1
0.5
0
0
100
200
300
400
500
600
700
800
900
1000
Generations

Figure 9

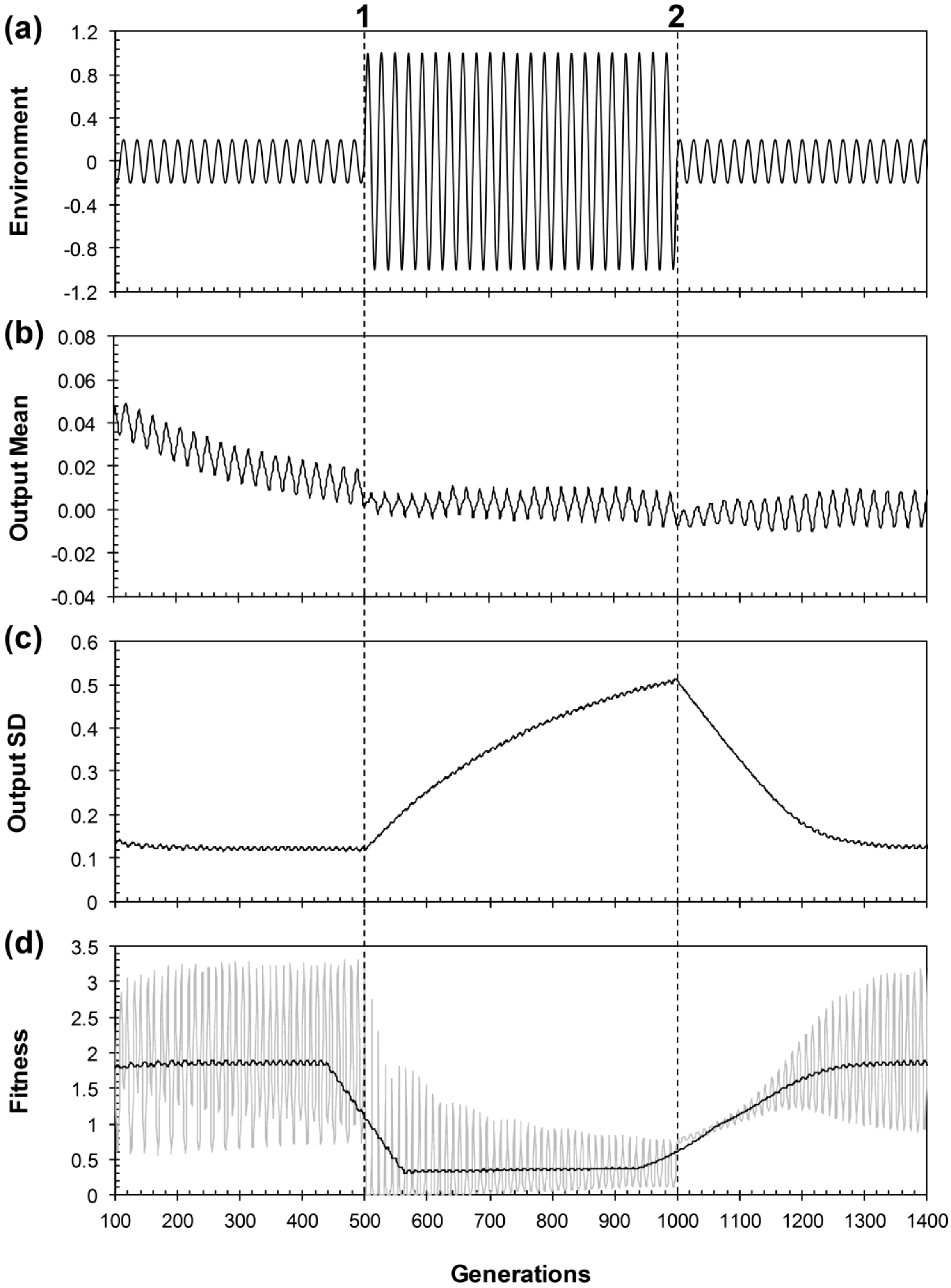
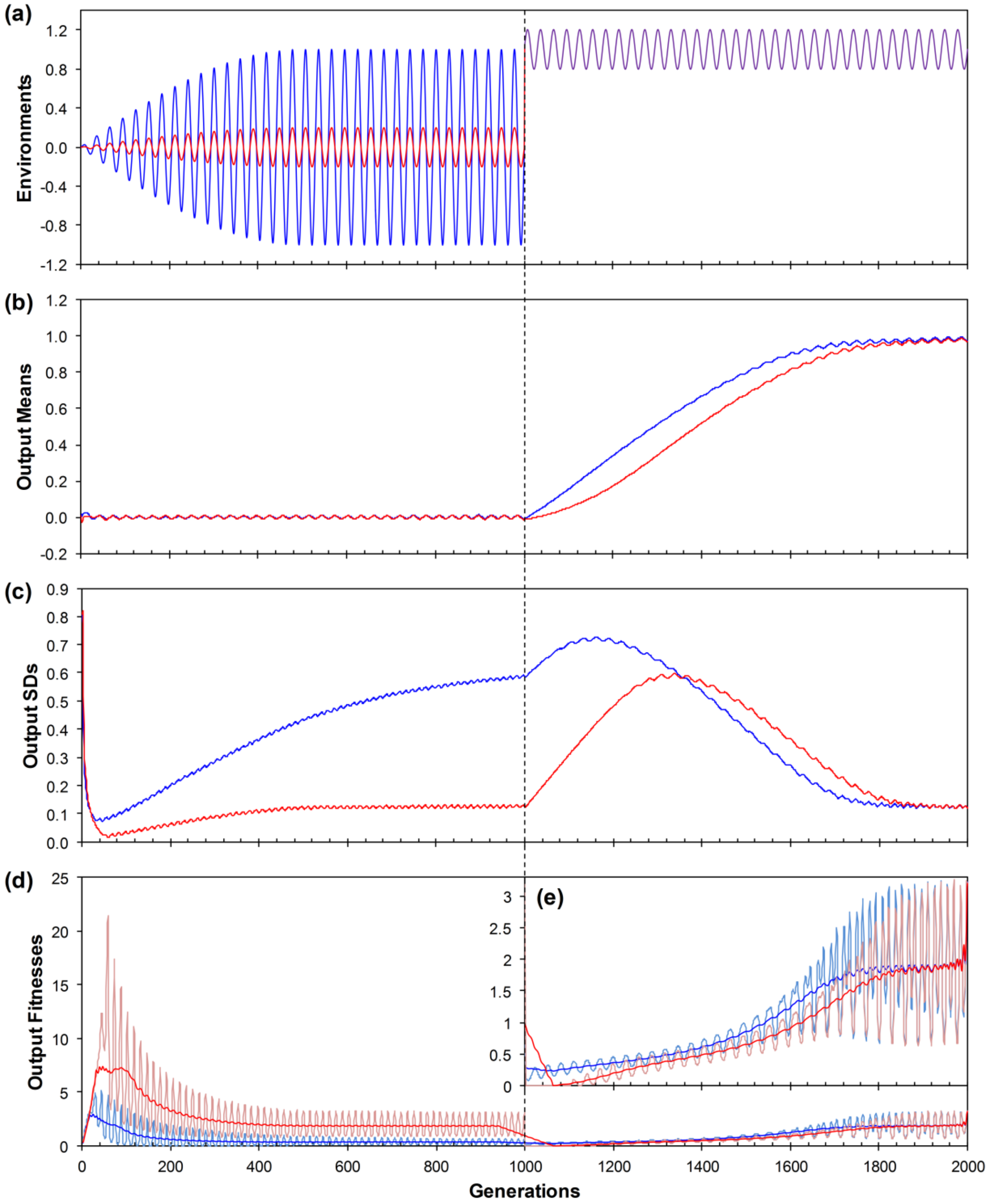
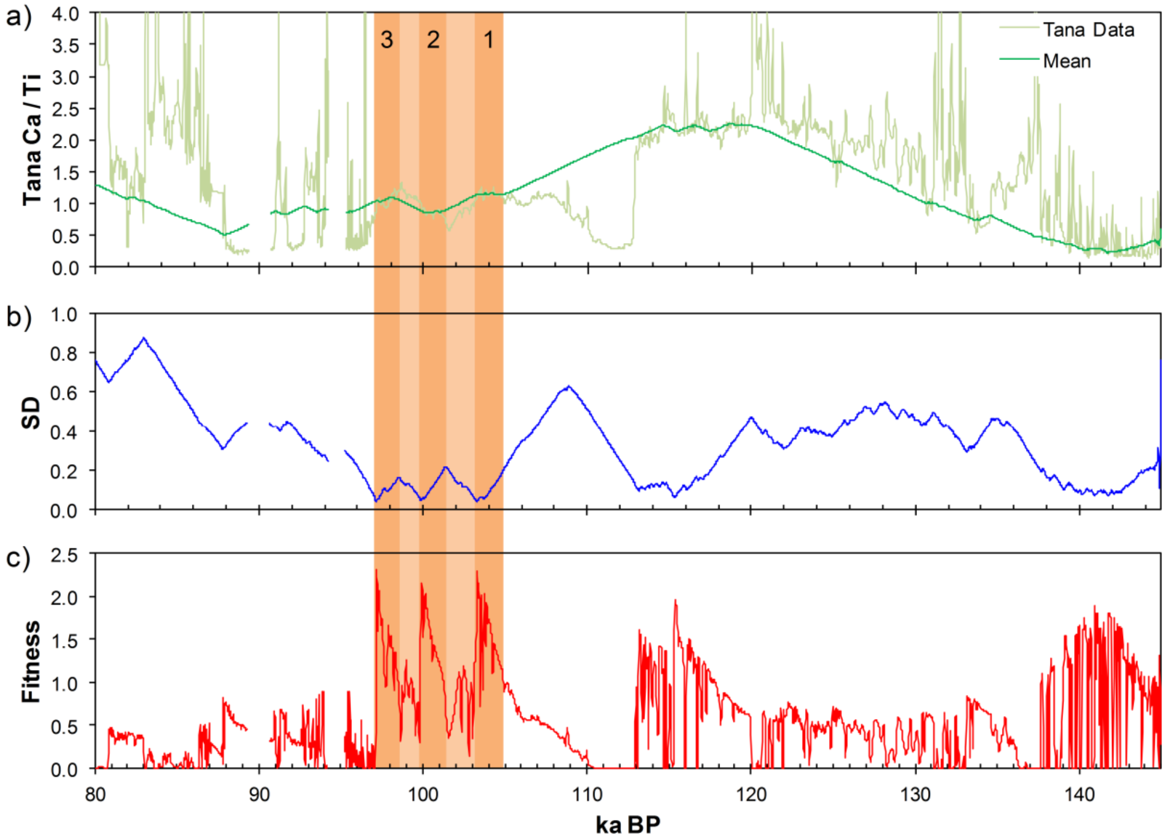

1
2
(a)
Environment
1.2
0.8
0.4
0
-0.4
-0.8
-1.2
(b)
Output Mean
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
(c)
Output SD
0.6
0.5
0.4
0.3
0.2
0.1
0
(d)
Fitness
3.5
3
2.5
2
1.5
1
0.5
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
Generations

Figure 10


(a)
Environments
1.2
0.8
0.4
0.0
-0.4
-0.8
-1.2
(b)
Output Means
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
(c)
Output SDs
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
(d)
Output Fitnesses
25
20
15
10
5
0
(e)
3
2.5
2
1.5
1
0.5
0
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Generations

1597 **Figure 11**



1598