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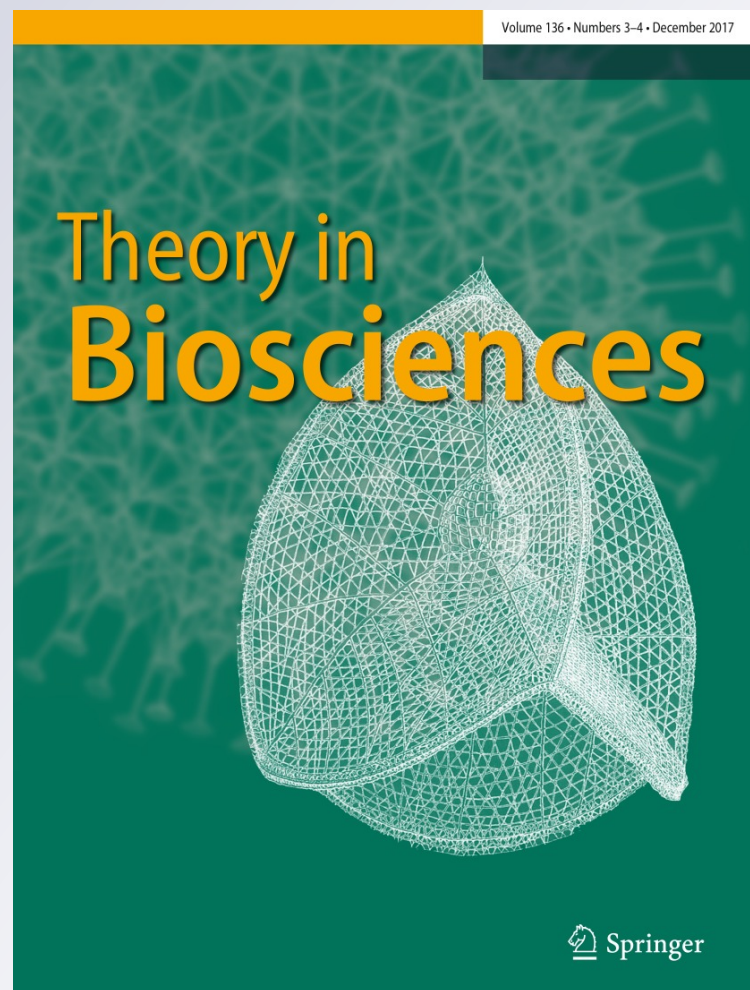
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Correlates and catalysts of hominin evolution in Africa

Jeffrey K. McKee^{1,2} 

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Abstract Hominin evolution in the African Pliocene and Pleistocene was accompanied and mediated by changes in the abiotic and biotic spheres. It has been hypothesized that such environmental changes were catalysts of hominin morphological evolution and speciations. Whereas there is little doubt that ecological changes were relevant to shaping the trajectories of mammalian evolution, testing specific hypotheses with data from the fossil record has yielded ambiguous results regarding environmental disruption as a primary catalyst. Proposed mechanisms for abiotic and biotic causes of evolution are not always consistent with the timing and trends exhibited by the African fossil record of hominins and other mammals. Analyses of fossil and genetic data suggest that much of hominin evolution, and by extension mammalian evolution, was autocatalytic, driven by feedback loops within a species or lineage, irrespective of changes in the external environment.

Keywords Autocatalytic evolution · Hominin · Climate change · Paleoecology

Introduction

The hominin phylogenetic tree is proving to be increasingly complex as it becomes better known through paleoanthropological excavations and analyses, supplemented by novel genetic data. The past decades have also witnessed a greater focus on ecological context of the hominins, raising questions regarding notions of direct environmental cause and effect in hominin evolution. If we are to make sense of the fossil record in a contemporary context, we must reconsider hypotheses concerning the evolutionary correlates and catalysts of past hominin diversification, speciation, and morphological trajectories.

In this paper my intent is to review and analyze three sets of hypotheses that are most discussed within the context of African hominin evolution: abiotic, biotic, and autocatalytic models of evolutionary change. Each set has strengths and weaknesses that can be tested, at least in part, with emerging fossil and genetic records. It is likely that all three played significant roles in shaping hominin evolution, but new views of how they did so can be refocused in light of the complexity of our human ancestry.

As an overview of the evolutionary model being developed here, consider the conceptualization in Fig. 1. Each ring represents a cross section of spheres of influence on hominin evolution in particular, and mammalian evolution in general. At the core is the genetic variability being influenced by the surrounding spheres through the forces of evolution (particularly natural selection, genetic drift, and gene flow, with mutation coming from within).

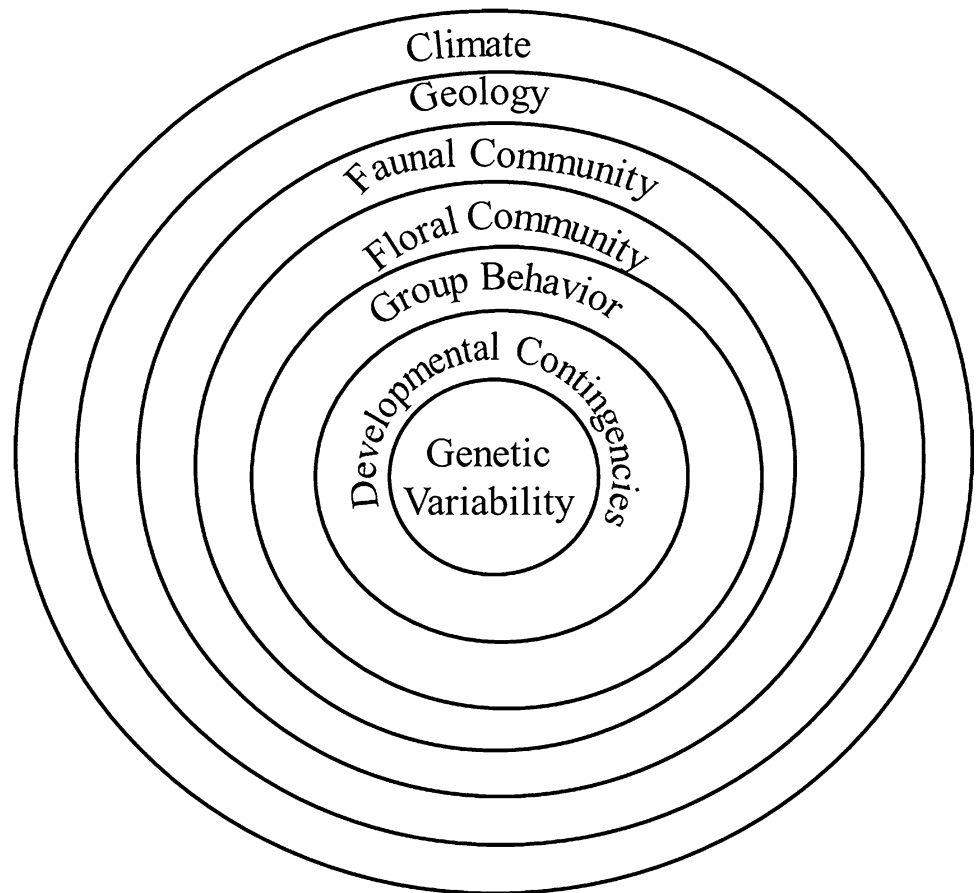
The outer spheres, climate and geology, are the abiotic influences. Here I will consider primarily climatic influences, as they have been the point of most discussion. This is not to dismiss geological influences, for which there is a

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Fig. 1 A model of spheres of influence relevant to natural selection among hominins and other mammals



growing appreciation (e.g., Bailey et al. 2011). But geological influences are often a partial cause or correlate of both global climate change (e.g., uplift of the Himalayas affecting global currents) or more local climatic change (e.g., tectonic uplift of the eastern portion of Africa and increased volcanism). Moreover, geomorphological changes often have the same effect as climatic changes in terms of fragmentation of populations (vicariance) or distribution drift of species of plants and animals.

The next two spheres are biotic, the faunal and floral communities, which have a more proximate influence on hominin evolution. Which sphere is more influential may vary depending on the phase of hominin evolution being considered. For example, in earlier phases when hominin diets consisted almost exclusively of vegetation, the floral community would perhaps be more vital than the faunal community, which would influence hominin evolution primarily through predation. As hominins moved into scavenging and then hunting niches, faunal interactions may have taken a greater role.

The inner spheres represent the keys to the autocatalytic model of hominin evolution (McKee 1999, 2000). This is the notion that contingencies of a species' development and behavior are the ultimate catalysts of evolution, and only

mediated by changes in their respective environments. Ultimately the genetic variability upon which natural selection acts comes from mutations or gene flow between populations of a species. For an individual to survive and reproduce, thereby contributing to the evolutionary trajectory of a population or species, it must be compatible with its own conspecifics developmentally, morphologically, and behaviorally. The inner spheres are where evolutionary novelties, or sometimes stasis, are initiated and maintained through feedback loops, and then shaped to varying degrees by the layers of surrounding spheres.

In some ways the three-dimensional representation of spheres of influence neglects a fourth dimension, representing interactions among the spheres at various levels. For example, climate and geology will affect the floral community, which in turn determines the composition of the faunal community. Likewise, keystone species of plant or animal may disproportionately influence the biotic sphere of a particular ecosystem, local climate, or even global climate, the latter of which appears to be the case with contemporary humans. Yet the spheres form a framework from which we can assess the degrees and modes of influence on hominin evolution, and work as a hypothetical starting point.

Abiotic models of hominin evolution

Darwin (1859) was adamant that the effects of climate on evolution were minimal, illustrating his point at length with the wide climatic ranges tolerated by many species. Yet climatic *change* and variability has long been correlated with hominin evolution, and began to be implicated as an ultimate *cause* of mammalian evolution in the Late Pliocene and Pleistocene of Africa (e.g., Brain 1985; Turner 1983; Vrba 1985a, b) or key factor that shaped the boundaries of evolution (e.g., Potts 1996a, b). Since the initial and important developments in evolutionary theory, particularly as applied to hominins, paleontologists and paleoclimatologists have accrued considerably more data with which to test these hypotheses.

The African continent, where our hominin ancestors first evolved, was affected by global, continental, and regional climatic change during key phases of hominin evolution (Boaz and Burckle 1983; Shackleton et al. 1984; Van Zinderen Bakker and Mercer 1986; Prentice and Denton 1988; Vrba et al. 1989; Partridge 1990; Shackleton 1995; deMenocal 1995, 2004, 2011; deMenocal and Bloemendal 1995; Bobe et al. 2002; Trauth et al. 2007; Donges et al. 2011; Levin 2015). The consequences of these changes have been viewed in terms of increased savannah grasslands and open habitats throughout the continent (Bonafille 1985; Vrba et al. 1989).

In assessing potential impacts on hominin evolution, one must be cognizant of variations in the broader continental trends. Analyses of paleosol carbonates in East Africa reveal no abrupt climatic events (Cerling 1992; Kingston et al. 1994; Levin et al. 2011; Levin 2015). However, as discussed below, there have been periods of increased climatic variability (Maslin et al. 2014).

In southern Africa there is only weak evidence for any marked climatic event around 2.5 Mya (millions years ago). It has been inferred largely from changes in the dominant bovid fauna between the times of Sterkfontein Member 4 and Sterkfontein Member 5/Swartkrans Member 1 (Vrba 1988). But a change in the dominant fauna represented within deposits at any one site may be explicable by changing taphonomic factors (Brain 1981; McKee 1991; McKee et al. 1995; O'Regan and Reynolds 2009).

Here I review two main sets of climatic hypotheses: the turnover-pulse hypothesis and variability selection.

Tests of the climatically induced turnover-pulse hypothesis

Vrba (1985a) first posited that global climatic events directly induced pulses of faunal turnover. In other words, rates of migration, speciation, and extinction accelerated in direct response to dramatic climatic shifts. The turnover-

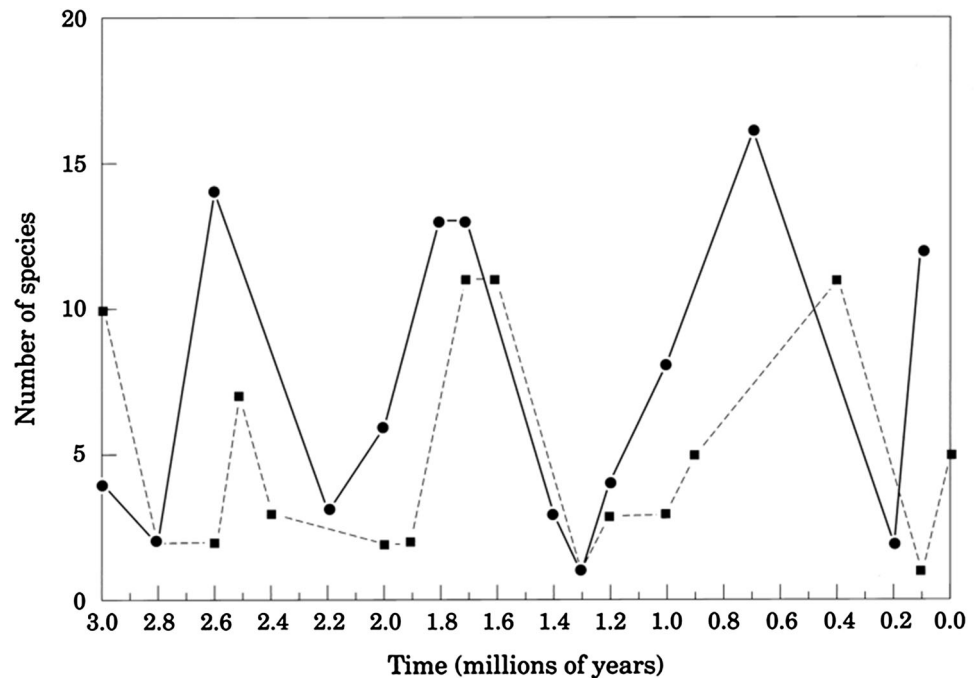
pulse hypothesis, a corollary of the punctuated equilibrium model, has been applied to the Late Pliocene origin of the genus *Homo* (Vrba 1985a, b, Vrba 1988; Hill et al. 1992; Schrenk et al. 1993; Bromage and Schrenk 1995). *Homo* “was born as part of this wave of change, to a world of drier conditions, a rather rapidly changing biota and a generally more challenging and exacting environment” (Tobias 1991: 138). A further putative climatic event in the mid-Pleistocene may have been related to the extinction of the robust *Australopithecus* lineages and geographic expansion of *Homo erectus* (Prentice and Denton 1988; Vrba 1988; Vrba et al. 1989), just prior to the emergence of archaic *Homo sapiens*.

Deductions from trends observed among the African bovidae formed the original basis of the turnover-pulse hypothesis (Vrba 1985c); correlations were then made with proxy evidence of paleoclimatic trends, inferred to be global trends. The basic hypothesis was that most faunal turnovers, i.e., regional origins and extinctions (including migrational and evolutionary occurrences), transpire in pulses of 100 Kyr (thousand years) or less in response to climatic events such as global cooling (Vrba 1985a). Vrba (1985a, 1988, 1993) and Turner (1990) suggested that pulses should affect a range of lineages, so the obvious testing ground would be regions in Africa in which the bovids and other mammalian families were migrating and evolving, to see if pulses can be detected in regional taxic turnover.

The turnover-pulse hypothesis initially seemed to have some support in Africa. A cursory look at trends in the fossil record of mammals from both East and southern Africa, displayed in the manner presented by Vrba (1985c) for bovids, demonstrates *apparent* pulses of first and last appearances (Fig. 2). One such ‘pulse’ coincides with the putative global climatic cooling ‘event’ around 2.5 Mya. A second apparent pulse around 1.8–1.7 Mya corresponds to the southern African appearance of *Homo erectus* (sensu Clarke 1985). A third pulse of first appearances at about 0.8 Mya and subsequent increased last appearances follows a proposed climatic event at 0.9 Mya (Prentice and Denton 1988), around the time of the first southern African appearance of archaic *Homo sapiens*. These correspond roughly to the three primary African climatic shifts cited by deMenocal (1995, 2004, 2011) and Levin (2015). But the points on the graph and, therefore, each of the apparent pulses, are determined by discrete events of fossilization at unevenly distributed times. The nature of the fossil record must first be assessed.

Recognition of putative pulses is limited by the imperfections of the fossil record: “... this imperfection is a great fact, which must be taken into account in all our speculations, or we shall constantly be going wrong” (Huxley 1894: 86). Because of the nature of the fossil record, the

Fig. 2 Number of first appearance dates (*circles*) and last appearance dates (*squares*) of Pliocene and Pleistocene large mammals in southern Africa, from 18 fossil assemblages Data from McKee et al. (1995), Turner et al. (1999), and Peart (2015)



turnover-pulse hypothesis, as it applies to Africa, also has its critics. Hill (1987), Kimbel (1995), and White (1995) acknowledge the inadequacies of the fossil record that could lead to spurious correlations. To be fair, Vrba (1985a) acknowledged early on the potential taphonomic and preservational biases, and took them into account in later work (Vrba and DeGusta 2000). Yet Bishop (1993) studied the suids fossil record of the East African Pliocene and Pleistocene, and found no evidence of pulses in turnover. Reed (1996, 1997) demonstrated only gradual change in mammalian morphological adaptations with the shift to drier climates in Africa. Behrensmeyer et al. (1997) studied the localized fossil record of the Turkana Basin and found a correlation between variations in apparent turnover and the number of localities per time unit, suggesting that the appearance of turnovers was an artifact of the uneven fossil record. Frost (2007) found no pulse in East African cercopithecids and suggested that their fossil record was consistent with a constant rate of turnover. Haile-Selassie et al. (2009) found faunal transitions in two late Miocene assemblages of the late Miocene, but were inconclusive about the plausibility of explaining them by climatic change, given the many complicating factors.

In the southern African context, Faith and Behrensmeyer (2013) found that among Quaternary ungulates of the Cape region, there were pulses of extinction but minimal evidence of speciation in association with environmental change. Most of the fossils in this region have been recovered from cave deposits, for which there are a wide variety of factors that may lead to deposition, preservation, and recovery of mammal bones (McKee et al. 1995). The

vast majority of the fossils are the inedible parts of animals that otherwise satiated the appetites of predators lurking near the caves. Assuming that such taphonomic factors are effectively random with respect to the origin and extinction of a species, it was possible to take them into account with simulated models of species turnover and bone deposition to predict how first and last appearances of fossil species correspond to true origins and extinctions. Expectations derived from these simulations could then be compared to the discrete points of time known from the fossil record.

Computerized models were used to simulate turnover among southern African and East African mammal species over a 3.2-Myr time frame (McKee 1995, 1996, 2001). The procedure was designed to couple theoretical rates of turnover in prehistoric mammalian communities with predictions for a fossil record of those communities. Fluctuations in observed first and last appearances were well within the range of simulated expectations, and close to the mean, both for models of constant turnover and pulsed turnover (with two exceptions noted below). The data lack enough resolution to rule out either model. Quite simply, the unequal distribution of fossil sites through time, and of animals identified from those fossil sites, resulted in pulses of sampling. Moreover, much of the turnover still has to be explained by other mechanisms, unrelated to ‘events’ of climatic change, as considerable turnover continues at times when there are no postulated pulses or major climatic events, particularly between 2 and 1 Mya.

There were two exceptions in both constant and pulsed models that were of particular interest in the East African data. At 2.5 and 0.8 Mya, the observed frequencies of

species last appearance dates exceeded those of the simulated models. This is evidence of a pulse of extinctions and/or extirpations that coincides with climatic shifts, an important point to which I will return.

More recently, Vrba (2005) conducted a pan-African test of the turnover-pulse hypothesis over the past 5 million years. The 0.5-Myr time intervals were considerably larger, thus removing the hypothesis from its original context. Moreover, although she detected large-scale pulses, there were no origination pulses detected after 2.5 Mya, eliminating from consideration all of the evolution within the genus *Homo* or the robust Australopiths. Clearly timescales of observation are important (e.g., Raia et al. 2005), and large timescales should be considered; “as over half of the fossil species of the past 3.2 Myr are extinct, it is conceivable the entire period represents an increase or pulse of turnovers within the greater context of geological time” (McKee 1996: 112). Larger timescales would remove the immediate relevance of the turnover-pulse hypothesis to the exigencies and timing of hominin evolutionary diversification, and finer timescales do not have the resolution needed for specific hypotheses (Kingston 2007).

Regional ecology and distribution drift

Dramatic climatic change should affect the structure of a local biotic community and the distribution of a species. But significant evolutionary effects may be lacking because species can migrate faster than climatic zones move (Raup 1991). Even the distribution of vegetation can respond quite quickly to climatic change (MacDonald et al. 1993). Mammals, being more immediately mobile than plants, could also undergo a distribution drift with climate change and find a suitable habitat within the mosaic without being forced into new behaviors and adaptations. A local fossil record would show turnover, but not necessarily evolution. Thus, one must question and assess the potential relevance of putative climatic change to the morphological evolution and speciations of mammals by dissecting out the components of turnover.

Turnover, as recognized in the fossil record, is a broad phenomenon inclusive of many transitions. Some of these are evolutionary, including speciation through lineal descent or phylogenetic divergence and transitional or terminal extinction. Migrations also play a substantial role in turnover, so if one is interested in examining climate as an evolutionary catalyst, the migrants must be weeded out. Turner and Wood (1993) have provided relevant data and analysis. For the period of 3.0–1.0 Myr, they tallied thirteen species that appear in the fossil record to have migrated from East Africa into southern Africa and six that have dispersed northwards. The apparent influx represents approximately 11% of the first appearances in southern

Africa during this time period. Nine of these first appearances are in the 1.8–1.5-Myr time range, when the most significant changes in biodiversity patterns were occurring in southern Africa (Turner 1990; Vrba 1985c) but with only gradual climatic change having been recognized or postulated. Assuming that the fossil data reflect the true migrational patterns to a reasonable degree, the remaining 89% or so of observed species appearances must be explained in terms of evolutionary origins of species.

Habitat changes induced by regional climatic change may lead to local or regional extirpations as opposed to terminal extinctions. Under conditions of climatic cooling over the past 3 Myr, many mammals could have moved north toward warmer, more equatorial regions. It is quite apparent that this has happened, as judged by modern animal distributions found in the study by Skinner and Smithers (1990) in comparison with data provided by the South African Weather Bureau. As one moves from the South African Cape near Elandsfontein, up to the Makapansgat hominin site in the Limpopo Province, the mean annual temperature increases by approximately 10 °C and the specific biodiversity of large mammals increases. Species known from the late Pleistocene fossil record of Elandsfontein in the South (Klein and Cruz-Urbe 1991), such as *Redunca arundinum* (reedbuck) and *Crocuta crocuta* (spotted hyaena), can now be found in the area of Makapansgat and further north but have long since disappeared farther south. From Makapansgat, to a distance of only 300 km to the northeast, the mean annual temperature increases an additional 3 °C. Here one can find natural populations of mammals known to have existed previously to the south for considerable time during the Pleistocene, including *Panthera leo* (lion), *Loxodonta africana* (elephant), *Ceratotherium simum* (white rhinoceros), *Diceros bicornis* (black rhinoceros), *Hippopotamus amphibius* (hippo), *Giraffa camelopardalis* (giraffe), and *Kobus ellipsiprymnus* (waterbuck). Whereas some of these may have been extirpated farther south during historic times due to human influences, some distributions appear to be related to climate. Thus, for example, still further north near the Okavango swamps in Botswana, one may find isolated populations of *Kobus leche* (red lechwe), known from within the last 100 Kyr at Equus Cave at Taung (Klein et al. 1991), which is now on the southeastern margin of the Kalahari desert.

A large number of Pliocene and Pleistocene extinctions, on the other hand, appear to have been terminal (data from McKee et al. 1995; Turner et al. 1999; Peart 2015). Of 149 large mammal species identified in the southern African fossil record, a total of 89 are extinct in southern Africa and 87 are terminally extinct. Thus, 58% of species extinctions must be explained on evolutionary grounds. Whether or not climatic change could have precipitated their extinctions remains to be seen.

The effects of climatic change are likely to include a considerable degree of distribution drift, and this may account for some of the turnover trends visible in the fossil record. Species need not adapt if they can follow their habitat. The remaining turnover, indeed the majority of what we see (89% of first appearances, 58% of last appearances), appears to have been the product of the evolutionary processes of speciation and extinction. Support for models of climatic causation of the evolutionary component of turnover thus requires postulation of potent evolutionary mechanisms.

Climate and mechanisms of causation

It is often noted that correlation does not necessarily imply causation. Thus, if climatic change caused evolutionary changes among the fauna, one must assess the potential mechanisms. As the climate changes, a number of fates can befall a species: (1) no change, as the species is equally well adapted in the habitat allowed by the new climate; (2) distribution drift; (3) terminal extinction; (4) evolutionary adaptation to a new habitat. The latter two are evolutionary occurrences for which we must find cogent processual explanations. If climatic change is to be postulated as the primary ultimate *cause*, then the proximate mechanisms must be able to account for the selectivity of evolutionary events among different taxa in different habitats at different times, for many species survive relatively unchanged through climatic oscillations while others evolve or go extinct.

Evolutionary origins of species may occur through vicariance, a mechanism that has been proposed in association with the turnover-pulse hypothesis. Under the vicariance model, subdivisions of species result through the shrinking of specific habitats into a patchwork distribution, as opposed to a cohesive shift of the habitat (Vrba 1985a, 1993). Brain (1985) has demonstrated how this could have happened with climatic change in the southern African context, and particularly how it may have affected vegetation distributions. The distributions of mammals with a high degree of habitat specificity or at least strong preferences for certain habitats would then become delimited by the ranges of the habitat islands, leading to the allopatry that may encourage speciation. Other abiotic processes may cause vicariance of mammals and allopatric speciation, such as tectonic movements, but climate could indeed be an important factor worthy of consideration and testing.

Some mammalian lineages would have a higher probability of vicariance than others (Vrba 1993). Thus, generally adapted, widely spread mammals would not be prone to speciation under this model, but others may. If the general climatic trend is one resulting in the spread of savannah grasslands and shrinking of forests and

woodlands, as had generally been seen to be the case, then certain predictions can be made of what to expect in the fossil record for more habitat-specific animals. For example, among the bovids, vicariance and thus speciation generally should affect woodland and forest browsers more so than most grassland grazers; likewise the browsers should be more vulnerable to extinction (Dodson 1989). Yet there is only one potential example among the browsers that fits the predictions of climatically induced vicariance. In the genus of browsers with the most species, *Tragelaphus*, two species date back to the time of Makapansgat Member 3 (approximately 3.2–3.0 Mya) and the other two immigrated from eastern Africa (Turner and Wood 1993). Vicariance is a possible explanation for the divergence of the immigrants, and climatic change is consistent with the extinction of *Tragelaphus pricei*. Indeed most browsers of the southern African fossil record have fewer species per genus, and have relatively greater species longevity, than grazers. This is despite many climatic oscillations that may have fragmented their habitats and indeed jeopardized their very survival. Perhaps the fossil record has missed many transitive browser species due to their isolation, but this seems unlikely given the occurrence of the other species of browsers at numerous fossil sites.

Generally adapted and widely distributed animals, such as the hominins, would have been least prone to vicariance (Kingston 2007; Grove 2011a). Even early hominins, including the robust *Australopithecus* (*Paranthropus*) species, are seen as being generally adapted and indeed adaptable (Brown and Feibel 1988; Sillen 1992; Wood and Strait 2004). At the outset of the apparent global cooling trend *circa* 3 Mya, *Australopithecus africanus* can be found in a sub-tropical forest environment at Makapansgat (Rayner et al. 1993). At Sterkfontein, sometime between 2.6 and 2.4 Mya, the species is found in a wooded environment sufficient for antelope to browse in dense bush (Vrba 1974, 1975, 1980). But at the same time, the Taung fauna and geological context may suggest a somewhat drier environment with extensive grassland cover, as indicated by the predominance of medium-sized alcelaphines (McKee and Tobias 1994) (*A. africanus* may predate the deposition of most of the Taung fauna, but the local environment in which it was found appears not to have changed dramatically; McKee (1993a, b). These varied environments thus challenge any notion of habitat specificity for the early hominin species of southern Africa. White et al. (1993) have found that *A. afarensis*, between 4 and 3 Mya in East Africa, also had a broad habitat range and endured significant environmental variability (Bonafille et al. 2004; Kingston 2007).

Likewise, during subsequent evolution of *Homo*, the hominin lineage found itself in a wide variety of climatic

regimes throughout Africa and beyond, through numerous climatic oscillations. Thus, climatically induced vicariance does not appear to have much potential relevance to hominin evolution in the sense of speciation via vicariance and genetic drift, but another angle on climatic variations is provided by the hypothesis of variability selection.

Variability selection

Variability selection, as introduced by Potts (1996a, b, 1998), is a complementary way to look at the influence of climate on hominin and mammalian evolution. The hypothesis centers on the notion that environmental variability on a large scale will favor generalized or ‘eurytopic’ species, and weed out more specialized or ‘stenotopic’ species. In other words, the process thus causes “habitat-specific adaptations to be replaced by structures and behaviors responsive to complex environmental change” (Potts 1998: 81). Potts (1996b) coined the term ‘versatilist’ to describe such mammals. Thus, the hypothesis focuses less on the speciation process, and more on the types and nature of species that make it through the evolutionary wringer.

Potts holds that key hominin adaptations occurred at such times of climatic variability. This notion has garnered support from Kingston (2007), Ash and Gallup (2007), Grove (2011a, b), Maslin et al. (2014), and further research from Potts (2013). Maslin et al. (2015) tied it to the turnover-pulse hypothesis. Kingston took it further, proposing the ‘shifting heterogeneity model’, stating that “In response to oscillating climatic conditions, patterns of heterogeneity were constantly shifting, resulting in continual flux of both plant and animal communities” (Kingston 2007: 24).

It is important to break down what kinds of specializations and generalizations are relevant to the hypothesis of variability selection. The focus could be not only on climate, but on dietary niches, habitat preferences, social and reproductive behaviors, or morphological characteristics. To wit, in testing speciation and extinction rates, Hernandez Fernandez and Vrba (2005) chose biomic specialization/generalization (stenobiomic and eurybiomic) as the relevant measures. As for morphology, Wood and Strait (2004) remind us that derived morphology does not necessarily equate with specialized adaptations. Hominins have highly derived brains, but that can lead to more generalized behavior or a more ‘versatilist’ adaptation (Potts 1996b, 1998; Grove 2011b). However, Gilbert (2008) questions whether ‘versatilists’ are individuals or species and has criticized Potts for conflating natural selection at organismal and species levels. Testing the hypotheses of variability selection can thus be challenging.

Considerations of stenotopy/eurytopy can lead to tautologous arguments. For example, it has long been

conjectured, even assumed, that the robust australopiths were more specialized than contemporaneous members of the genus *Homo* (Gundling 2005; Delisle 2007). This would appear to support the hypothesis of variability selection, as they went extinct whereas the more generalized members of *Homo* survived. But just because the former went extinct does not necessarily mean that they were more specialized in any of the manners described above. Wood and Strait (2004) tested this notion with comparisons of *Homo* and what they generically refer to as *Paranthropus*. They found only one trait of *Paranthropus*, that of occlusal morphology, in which stenotopy was consistently more in evidence than in *Homo*.

Summary of abiotic catalysts

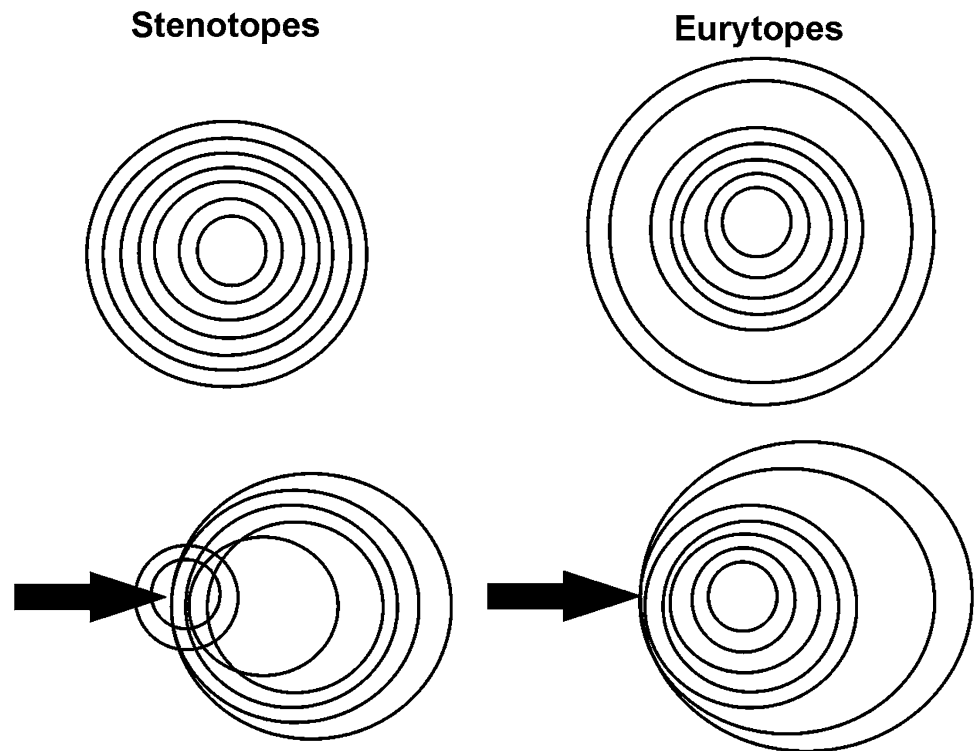
Under the guiding model proposed in Fig. 1, we can compare the effects of abiotic change on stenotopes vs. eurytopes (Fig. 3). Climatic and geologic changes, the outer spheres, have very little effect on the eurytopes, as their adaptability represented by the inner spheres is not impinged upon. There are two possible results for the stenotopes, depending on the size of the core spheres of genetic, developmental, and behavioral variability: one is survival of a reduced population of those in the range of adaptation, the other is extinction. Given the data presented earlier with excess extinctions in East Africa (McKee 2001), the evidence would tend to suggest that extinction is the more likely option (see also Faith and Behrensmeier 2013).

Despite the difficulties in dissecting out elements of stenotopy and eurytopy, and applying them to species of the African fossil record, one must add one more caveat. Environments are constantly changing over the long term in not only the abiotic spheres, but also in the biotic spheres, and thus eurytopes should almost always be favored, irrespective of climate change. This is explored in the next main section. Moreover, if there were only effectively neutral environmental change in all spheres, one could still argue that eurytopes would be favored as well due to the niche expansion and radiation afforded by the generalized adaptability, i.e., autocatalysis.

Biotic models of hominin evolution

Life for most mammals involves intensive ecological interactions with other creatures; that much is clear. How such interactions work, even among modern communities, is remarkably unclear (Pimm 1991). As the biotic community forms the immediate interactive environment of a species, such as an early hominin, there is little doubt that it may help to shape the course of the evolution of a lineage,

Fig. 3 Climatic and geological shifts and the effects on stenotopic vs. eurytopic species



but again the mechanisms are difficult to assess. However, the central issue to be addressed here is even more basic: that of species interactions as potential evolutionary catalysts.

Community evolution may provide a basis for analyzing and understanding the specific problems of human evolution (Foley 1984). In this sense, the driving force behind species evolution would be biotic rather than abiotic. The mechanism most often cited to catalyze this system, in the absence of abiotic forcing, is interspecific competition (e.g., Winterhalder 1981). This may take the shape of Van Valen's (1973) 'Red Queen's Hypothesis', which Stenseth and Maynard Smith (1984) have shown to be a plausible mechanism for propelling evolution at a steady rate in the absence of external physical change. The Red Queen's model involves a veritable arms race of adaptation among competitors and upmanship in predator/prey, parasite/host, and other ecological relations. Because commensalism and mutualism conceivably could cause evolution as well, one should test the comprehensive concept of a 'species interaction hypothesis': ecological interactions among members of the biotic community are sufficient to catalyze the evolution of the component species.

Predictions for the fossil record

Analyses of the African fossil record may be used to test predictions of generalized evolutionary trends expected through catalysis by species interactions. Extrinsic biotic

causes of speciation and extinction, which have been given the appellation of 'weak environmentalism', were rejected by Vrba (1985a) on the grounds that most appearances of new species should be random with respect to time. Vrba opted for 'strong environmentalism', that of abiotic causation, as a single extrinsic cause would be needed to account for the large numbers of simultaneous speciations and extinctions. This overlooks the possibility of the cascade of effects throughout the food web and beyond a local ecosystem that could occur with the addition or removal of a keystone species. In any case, a random distribution of turnovers through time, primarily speciations and extinctions, can account for the trends observed in the fossil record, as noted above (McKee 1995, 1996; Peart 2015). This fulfills the prediction of temporally random appearances and disappearances of species. Thus, the southern and East African data strengthen the case for weak environmentalism, and weaken the case for strong environmentalism.

Unequivocal evidence for the consequences of past interactions among species may be difficult to find. However, the fossil record presents a number of cases of extinction that have been interpreted in terms of species interactions. One such notion is that the entry of early humans into the guild of carnivores led to competition and a subsequent decline in the number of large carnivore species, coinciding with the emergence of the genus *Homo* (Walker 1984; Klein 1992). It has also been posited that the reduction in numbers of cercopithecoid species was due to

competition with the omnivorous hominin lineage during the *Australopithecus* to *Homo* transition (McKee 1991, 2007). The eventual expansion of *Homo erectus* may have also been a contributing factor to the extinction of *A. robustus*, through competitive exclusion (Klein 1988). Although there are other hypotheses, these three have been chosen because they have one thing in common: anthropogenic causes of evolution, and in particular, competition leading to extinction.

Ecological correlates of evolutionary trends are difficult to interpret because we are only seeing a small component of the biotic community in the fossil record. One small virus among large carnivores, or the spread of one tasty but poisonous plant into primate habitats, could easily result in the kinds of trends we see. Bender et al. (1984) noted an example in which the introduction of white-tailed deer to Nova Scotia in 1894 and subsequent extinction of caribou may have appeared to be competitive exclusion, but was more likely due to differential susceptibility to a meningeal parasitic nematode. Even among the species that are visible in the fossil record, first and last appearances do not necessarily correspond to origins and extinctions, so false correlations of simultaneous events are likely (McKee 1995, 1996, 2000, 2001).

Doubts about the validity of species interaction hypotheses have been expressed by Turner (1990) due to the perceived lack of a cogent mechanism, particularly in the case of extinctions in the large carnivore guild. But ecological studies of contemporary populations have shown interspecific competition to be common, and have elucidated a number of mechanisms for changing population densities as well as lifestyles of the competitors (Schoener 1983; Connell 1983; Sih et al. 1985). There is no reason why these principles cannot apply to larger scale phenomena. On the other hand, it is not clear how pervasive interspecific competition may have been. Furthermore, in many life forms, intraspecific competition is most often as strong or stronger than interspecific competition (Connell 1983). If this applies to terrestrial mammals, then Darwinian intraspecific competition may still hold the key to understanding trends in evolution.

Evolutionary consequences of interspecific competition, or even of predator/prey relations, are difficult to predict due to the richness of potential species interactions, direct and indirect (Bender et al. 1984; Sih et al. 1985; Yodzis 1988; Pimm 1991). Translating the implications of ecological studies into principles for understanding interactions among species in the fossil record becomes quite problematic. There are known ecological mechanisms for competition to lead to extinctions, and certainly these were in operation in the past, but it will be exceptionally difficult to correctly associate any particular mechanism with the extinction of a particular species. Although the causes may

not be knowable in detail, general tests of the notion that competition led to some extinctions may be possible. Indeed the Red Queen's hypothesis predicts constant rates of extinction (Van Valen 1973), as supported by the southern and East African fossil data.

Van Valen's (1973) law of extinction may explain some trends in the fossil record, but comparable mechanisms for species interactions to cause speciation, as opposed to extinction, are less abundant or less obvious. Extrinsic biotic changes conceivably could lead to vicariance and allopatric speciation, but still the explanatory value of vicariance alone is dubious given the patterns in southern African fossil record. The question then arises as to how a conservative process such as natural selection, which tends to reduce variability, could lead to widespread progressive evolution and speciation during a time of environmental change in the living world.

Causation in the biotic sphere

There are many clear cases in nature where an evolutionary trend is due to natural selection through interactions with other species. Coevolution (Ehrlich and Raven 1964) provides one type of example, and has garnered significant support (Janz 2011). But without observed behaviors and interactions, such trends are difficult to detect and test in the fossil record. One clear example from the fossil and archeological record of change in one species leading to changes in others came at the origins of agriculture. Before human intent was placed upon plant and animal reproductive patterns with the accrual of knowledge regarding selective breeding, plants and animals essentially evolved to become more attractive to humans as a response to shifts in human behavior.

Hominin evolution has often been at odds with such trends of evolving to fit the community landscape. For example, bipedality is a great hallmark of hominin evolution, but it is a slow mode of locomotion relative to virtually all medium- to large-size carnivorous mammals and leave hominins quite vulnerable to predation, more so than in other primates. Increasingly altricial young are at risk for longer periods of time, slow down the family or troop, and are more difficult to carry.

On the other hand, an increase in body size that was evidenced by *Homo erectus* could have made individuals look less vulnerable, given greater strength to ward off predators, allowed longer distance running (Bramble and Lieberman 2004), and even the ability to face off predators by running backward (McKee et al. 2008). Yet there were no significant changes in the African fossil record of predators to suggest that the hominins had to adapt to something new in the biotic landscape. Indeed, viewing *H. erectus* as part of the surrounding biotic sphere of other

animals, the evolution of *H. erectus* may have been the key change in the biotic sphere that led to the extinction of other animals, particularly large carnivores and cercopithecids (Klein 1988; McKee 2003).

Given that species interactions are rarely testable in the fossil record, we must rely on our knowledge of proposed mechanisms for evolutionary change. On this basis I would postulate that the impacts of changes in the biotic environment, like that of the abiotic, is more a driver of extinction than of evolution. This is consistent with van Valen's (1974) law of constant extinction. Figure 4 is a representation of the impact of the biotic sphere. Only those with enough genetic variability, behavioral adaptability, or eurytopic qualities would survive and or adapt morphologically.

Autocatalytic models of evolution

Evolution does not necessarily need an extrinsic cause or catalyst. Here I expound the hypothesis that most of Neogene mammalian evolution is autocatalytic: one evolutionary step within a species is the only necessary catalyst of the next step. An evolutionary advance may free an organism for more structural and behavioral possibilities, or may impose constraints on progress in certain directions. There is no doubt that extrinsic influences may help to shape the course of specific adaptations by establishing selective parameters, but environmental change need not be the initiating *cause* of evolution. Evolution is its own

cause, and continues with or without extrinsic environmental change.

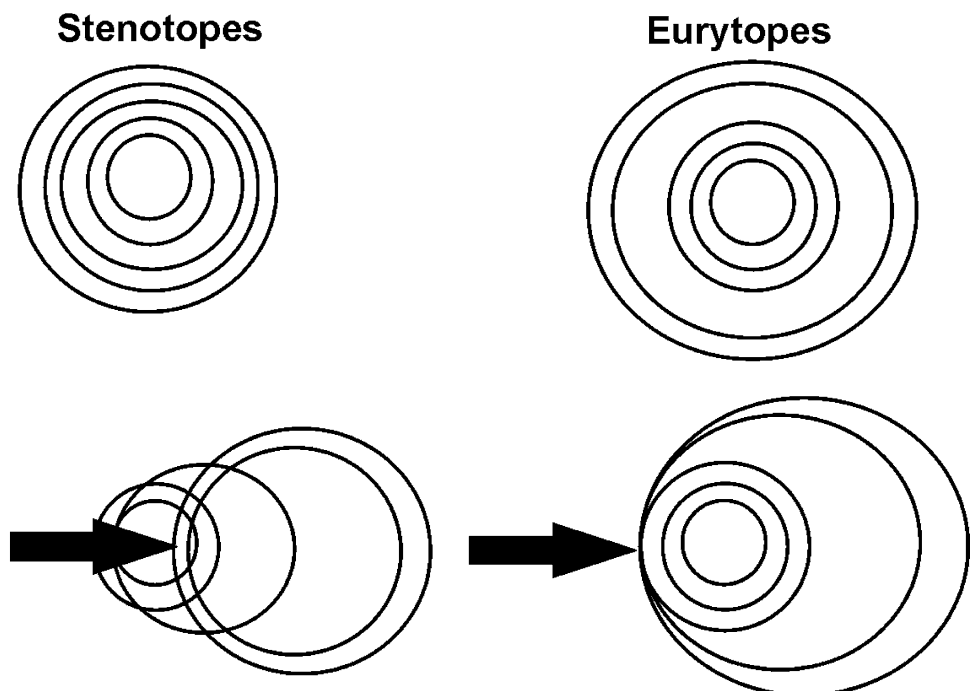
Like other causal explanations of evolution, this notion of autocatalytic evolution is not new, having its own foundations at the inception of Darwinism. Thomas Huxley, in 1878, put forth the following reservation about natural selection that is still relevant to consider today:

“How far ‘natural selection’ suffices for the production of species remains to be seen. Few can doubt that, if not the whole cause, it is a very important factor in that operation; and that it must play a great part in the sorting out of varieties into those which are transitory and those which are permanent. But the *causes* and conditions of variation have yet to be thoroughly explored; and the importance of natural selection will not be impaired, even if further inquiries should prove that variability is definite, and is determined in certain directions rather than others, by *conditions inherent in that which varies*” (Huxley 1888: 306–307, italics mine).

The neo-Darwinian synthesis answered Huxley in part, for genes certainly establish the limits of variability and mutations are the ultimate catalysts of evolutionary change. But further “conditions inherent in that which varies”, such as the novel structural characteristics that commanded Huxley's attention, may themselves cause or catalyze further evolutionary change.

Even though the concept of autocatalysis has been well established, it has received scant attention in the literature.

Fig. 4 Faunal and floral shifts and the effects on stenotopic vs. eurytopic species



Autocatalysis is usually relegated to discussions of the origins of life (e.g., Reid 1985; Brooks and Wiley 1988; Kauffman 1993; Hordijk et al. 2010), or to concepts of selective feedback loops in the acceleration of human brain evolution (Bielicki 1969; Godfrey and Jacobs 1981; Tobias 1981, 1994; Henneberg 1987, 1992). The general term ‘autocatalytic evolution’ is used to fill a void in the lexicon of evolutionary research. Autocatalytic evolution is proposed here as a process and an initiating cause of evolutionary dynamics. Hypotheses that can be constructed to test it are consistent with, and indeed necessitate, a pluralistic approach with a wide variety of research strategies (see Wake 1991).

The models of abiotic and biotic forcing of evolution discussed above have the common theme of stresses from environmental change resulting in intensified natural selection. But the greatest changes visible in the fossil record of southern Africa, at least in terms of biodiversity patterns, occur over an extended period of apparent climatic calm between 2 and 1 Myr (Levin 2015). So first one must question whether an increased intensity of natural selection from external influences would result in such changes, or if exactly the opposite, a relaxation of negative selection during a time of relative environmental stability and subsequent autocatalytic evolution, may promote the evolutionary novelties by which paleontologists recognize species.

Mechanisms of autocatalytic evolution

The basis of autocatalytic evolution depends not so much on natural selection alone as it does on the varied effectiveness, direction, and relative applicability of natural selection. Under the shifting balance theories of Wright (1932, 1977), the deterministic forces of selection interplay with stochastic events for an organism to move across an adaptive landscape. But the fitness peaks and saddles of the landscape are controlled by the nature of the organism, more so than by the environment. For example, changes in selective values of traits could be due to the pleiotropic effects of related traits. As Mayr (1991: 87) states, “It is not the environment that selects, but the organism that copes with the environment more or less successfully. There is no external selection force”.

An important hallmark of hominin evolution over the past 3 Myr has been the continuous expansion of the brain, particularly in the development of the mammalian neocortex. The behavioral plasticity that accompanied brain evolution is what changed the adaptive milieu of early humans. The environment could be sought by foresight and, eventually, manipulated by tools. For example, in their tests of the variability selection hypothesis, Ash and Gallup (2007) show correlations between the brain size of *Homo* and colder or more variable climates. But was it the climate

that led to brain size selection, or the brain advances that led the genus *Homo* to venture into new and more variable climates? Evolution could then proceed through positive natural selection for better brains and relaxed selection for features that directly interfaced with the environment (Bielicki 1965, 1969; Mayr 1970; Holloway 1972; Tobias 1971, 1981, 1994; Henneberg 1987, 1992; McKee 1999, 2000). Likewise, one may predict that as the fossil record of hominin morphology is extended further into the past, the hallmark of hominin origins, bipedality and orthograde posture, will be shown to have increased hominin adaptability through extensions of exploitable habitats (Hunt 1994) and will be a consistent morphological correlate with potential for brain expansion. In other words, evolution itself led to further evolutionary potential.

Rather than negative natural selection working through the elimination of the unfit, as in the models of environmental forcing discussed above, autocatalytic evolution through positive natural selection may operate simply through increased longevity and fecundity. Those hominins who could manipulate the environment, whatever environment it may be, and perhaps even help the survival of mates and offspring through social cooperation would effectively select themselves for the greatest contributions to the lineage. That this force was strong is evidenced by the consequences, maladaptive in and of themselves, of increased infant dependency and, at least in modern humans if not earlier, tremendous obstetric problems with the birth of a large-brained infant (Trevathan 2010). It was the eurytopic adaptability inherent in humans with complex brains, not changes in the external environment, that allowed these vulnerable consequences.

Environmental manipulation would have had the further effect of relaxing natural selection for those features that had been more directly related to the extrinsic features of the environment. For example, bipedality could remain a slow form of locomotion without a need to quicken the pace to escape predators, as novel strategies for group defense could be used, especially with tool use. The masticatory system could reduce the specializations of the grinding apparatus to a smaller teeth and jaws for which a diet could be chosen and, eventually, processed. This relaxation would have reduced the ‘complexity crisis’ (Kauffman 1993; McKee 2000): the stasis that results from complex interactions of sustained selective forces on many independent features, disallowing genetic and morphological or physiological ‘exploration’ of the adaptive landscape. A more variable set of morphological structures, as we see from the times of early *Homo*, may have resulted from such relaxed selection.

By chance, some new adaptations could have arisen that would have been subjected to positive selection. “In

this sense chance means that a variation having appeared, *chanced to find a suitable environment*” (Morgan 1910: 203). In other words, all adaptations were exaptations that became useful. But the behavioral change of a species must be permitted by existing variants of both structure and behavior; it becomes apparent in the fossil record when positive natural selection enhances, and perhaps by chance refines, a structure throughout the population. And, in some cases, morphological change itself may permit the new behavioral repertoires (Wake 1992). Thus, evolution continues not so much because natural selection adapts organisms to the extrinsic challenges of their environments, but because organisms find ways to use their features to fit an environment to themselves. In this view of evolution, invention is the mother of necessity.

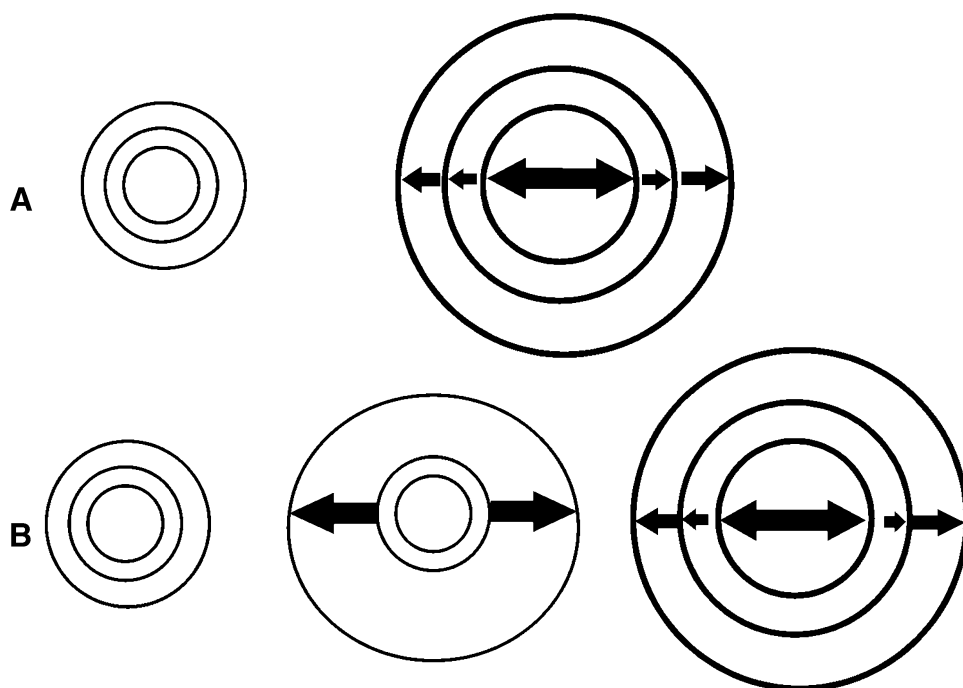
The causal route in the autocatalytic model is inverted and multidimensional, as illustrated in Fig. 5. As with all models discussed here, evolutionary novelty must ultimately be initiated at a genetic level. The path it takes toward success or failure is a bit different, however, under autocatalysis. A novelty first has to go through developmental constraints and contingencies. It might get quashed there and lead to further stasis, or expand the sphere to be less constrained. In a successful species, i.e., one that has a growing population, there are more opportunities for genetic novelties and more for natural selection to work with. Success in this sense would breed greater potential for future advances, as part of a positive feedback loop.

The outer sphere of the autocatalytic realm, that of group behavior, can release both developmental contingencies and genetic opportunities. In this sense, the behavioral generalist always has the advantage. When this involves movement into a new ecological niche, often the initial changes are behavioral, followed by structural modification (Mayr 1970).

The key to understanding autocatalytic evolution is that the inner spheres control the destiny of a species, not *changes* in the outer spheres. The outer spheres are certainly relevant to the ultimate trajectory of a species, but self-developed propensities and challenges configure the generational nuances of the evolutionary process.

Well-known examples and mechanisms of evolutionary change among mammals may also be characterized as autocatalytic processes. For example, Darwin (1871) introduced sexual selection as an evolutionary mechanism that operates on the basis of morphological and behavioral aspects intrinsic to a species. Fisher (1958) demonstrated the potentially profound and rapid morphological effects of sexual selection. Lovejoy (1981) has argued in effect that sexual selection was responsible for the evolution of the epigamic features of humans; although this may not be testable or even recognizable in the fossil record, it still presents a plausible form of evolution, and perhaps even speciation, based on the intrinsic features of the species behavior and morphology. Likewise, the horn-core shapes of some bovids, by which paleontologists recognize different species, may be the product of sexual selection, mate recognition, or intraspecific dominance

Fig. 5 Interactions of the autocatalytic spheres of evolution, from outside in: behavioral, developmental, and genetic. **a** Autocatalysis initiated by increase in population and/or genetic diversity, allowing developmental and behavioral novelties. **b** Autocatalysis initiated by behavioral change and niche building/diversification, expanding genetic and developmental possibilities



behaviors. Although some horns may be used for defense or in relation to other extrinsic factors, the variants are primarily selected (or allowed) by factors intrinsic to the bovid species.

If species adaptations were generalized enough to allow entry into numerous habitats, as was the apparent case with the hominins, or the environment to which they were adapted was sufficiently widespread, as may have been the case for some grazing bovids, then population size may increase. With a larger population there are greater chances for new variants to arise, either as new genes or new gene combinations. Some of these may be of selective value within the population, and as they spread throughout a population or species, they would be visible in the fossil record as evolutionary change, and perhaps even used as a defining characteristic of a new species. Other variants may allow possessing members to venture into new niches in different habitats, leading to new selective parameters, isolation from the source population, and eventual speciation.

The causes of stasis may also be autocatalytic, having arisen from structural constraints inherent in the organism (Thompson 1942). This has been noted on a more general level by Thomas and Reif (1993: 353): “The constraints of geometry, growth patterns and raw materials... constitute formal causes of skeletal design”. Further constraints may arise from stabilizing natural selection (e.g., Gingerich 1993), which will maintain good adaptations if a reasonable (or near ‘optimal’) fitness peak has been achieved. If multiple selective pressures led to either high fitness or a sub-optimally fit complexity crisis from which a species cannot evolve, the species would have got to that point by its own evolutionary devices. With severe environmental change, if the adaptations are specialized or restrictive, extinction would be more likely than speciation; the entire available adaptive landscape would have been lowered.

Hypothetically, the case of the carnivores may demonstrate both extinction and stasis through autocatalytic evolution. The extinction of the large carnivores, be it associated with environmental change or not, may simply be a case of ‘bad design’. Large carnivores rarely fare well for long (Colinvaux 1978). McCann and Yodzis (1994) produced an ecosystem model in which top predators went suddenly and inexplicably extinct without any perturbation to the ecological system. Likewise, the apparent stasis of many of the surviving carnivores may be due to the pressures of life at the top of the food web. For some carnivores, their adaptations were so successful, such as those of the leopards, that selective forces maintained their features. Alternatively, a complexity crisis may have developed from the simultaneous selection pressures needed to maintain a functional system of speed, behavior, and dental specialization.

Hominin examples of autocatalytic evolution

It is now clear that origins of bipedality predated the global and African climatic shifts once thought to have caused this hallmark of hominin evolution (White et al. 2009). Moreover, it was not a sudden shift in morphology after hominins diverged from chimp ancestors, but phased in through facultative bipedality (Lovejoy et al. 2009). There are a range of autocatalytic hypotheses, many of which focus more on consequences of orthograde posture more than advantages in locomotion. These include the freeing of the hands (Darwin 1871), sexual selection and provisioning behaviors (Lovejoy 1981), terrestrial feeding postures (Hunt 1994), and developmental correlates with brain evolution (McKee 1999, 2000). These remain speculative and in need of further testing, so it is worth looking at other key hominin developments where we can tie new genetic data to morphological and archeological evidence.

Although the phylogeny of known hominins has become increasingly ‘bushy’, at the core of human evolution is a continuous line of descent, irrespective of speciation ‘events’ and divergences toward populations or species that went terminally extinct. Since our hominin divergence from chimp ancestors, roughly 6 Mya, that core has accrued two significant sets of mutations in non-protein coding genes. Human Accelerated Region 1 (HAR1) is a series of 118 base pairs of DNA, showing 18 differences between modern chimps and humans (Pollard et al. 2006). This had been a highly conservative area of the genome, such that differences between chimps and chickens showed only two base pair differences. It turns out that this region is involved with RNA in neuronal development of the human brain’s cerebral cortex. The accrual of these mutations and their continual selection, along with other genes involved in brain evolution (Vallender et al. 2008), is statistically unlikely to have been at speciation events, but at the core line of hominin evolution, with some coming to be fixed in modern humans (Burbano et al. 2012). Under a model of autocatalytic evolution, one of the 18 mutations, fixed in the population by natural selection, allowed more to function, irrespective of *changes* in the abiotic or biotic environments. This can be tested by investigating whether or not there was a cascade effect of development; if not, then autocatalysis may not be the best explanation.

At some point in the past there was an important alteration in hominin dietary behavior. Early *Homo* began scavenging meat and eventually went to hunting. This change in behavior altered the selective conditions for teeth (molars could get smaller), and consequently the face, along with body size and body composition. It may also have been a component favoring selection for increased encephalization and brain complexity. This shift was aided and accompanied by stone tool manufacture and use. This

is where Human Accelerated Region 2 (HAR2, also known as HACNS1) may have played a role. There were rapid changes in this otherwise conservative region of the genome that is involved with the development of the wrist and thumb (Prabhakar et al. 2008). These 16 base substitutions, out of 546 base pairs, underwent positive selection to become fixed in human populations (Hünemeier et al. 2010). If the wrist changes can be further associated with grip, then it can be interpreted as a 'tool making' gene, which would have been favored in selection as a result of novel behaviors in early *Homo*. Observations by Davidson and McGrew (2005:813) bear out the autocatalytic nature of these events: "the act of knapping created a new niche for hominins". The feedback loops between hominin brains, hands, and behavior is apparent in our genes and our morphology.

Wrangham and Carmody (2010) have taken such notions further with their "control of fire hypothesis". They suggest that fire use was a prerequisite for the obligate terrestriality of *Homo erectus* due to the need for protection from predation. The benefits of fire use in cooking meat, such as softer food, higher nutrition, and less disease, would allow or even catalyze selective advantages of changes in the teeth, gastrointestinal tract, and brain. They might be correct, given the mounting evidence for the controlled use of fire at South African fossil sites of Swartkrans (Brain and Sillen 1988; Brain 1993) and Wonderwerk Cave (Bernaa et al. 2012), both of which are associated with *Homo erectus*.

More recent trends in human evolution show that dietary changes can rapidly alter the selective environment for human physiology, resulting in gene–culture coevolution (O'Brien and Laland 2012). Two examples stand out. Those populations who have longer histories of dairy milk consumption have higher frequencies of lactase persistence into adulthood to digest the lactose in milk (Bersaglieri et al. 2004). This apparently happened independently in both Africa and Europe (Tishkoff et al. 2007). Likewise, the advent of crop agriculture leading to greater consumption of starch-rich foods led to selection for the multiplication of *AMY1* genes to produce more salivary amylase for starch digestion (Perry et al. 2007). These genetic adaptations provide unequivocal evidence of autocatalytic evolution initiated by human behavioral changes and niche construction.

Conclusions

Apparent environmental change accompanied the evolution of the hominin lineage in Africa. The types of mammals with which early humans would have interacted

developed novel characteristics and the community structure of large mammals evolved as well. Meanwhile the global climatic fluctuations gradually trended toward cooler temperatures, and along with tectonic activities affected the interior of the African continent and the distribution of the animals within it. These ecological correlates of hominin evolution, however, did not necessarily constitute a cause or catalyst of evolution.

Causal models of mammalian evolution were tested by analysis of trends in the fossil record. The African data of the late Pliocene and Pleistocene offer no support for models of extrinsic causation. Putative climatic events cannot be empirically or logically justified as evolutionary catalysts, with the possible exceptions of some extinctions. The turnover-pulses that were to have accompanied the events can be shown to be more apparent than real, as mere artifacts of an incomplete fossil record. The same lack of completeness in the preservation of past biotic communities thwarts scientific testing of extrinsic biotic catalysts.

A lack of supporting evidence, of course, is far from disproof of extrinsic catalysts of evolution. However, the lack of effective explanatory mechanisms is a serious deterrent to their broad acceptance. Furthermore, the data run counter to some of the general predictions of extrinsic causation models. Thus, we see that apparent stability of the climate and expansive niches were associated with the greatest degree of evolutionary innovation and speciation. This suggests that evolutionary change may proceed, even flourish, without extrinsic forcing.

Ultimate catalysts and mechanisms of evolutionary change may come from within lineages, shaped and allowed by both intrinsic and extrinsic exigencies. The notion of autocatalytic evolution is consistent with the fossil and genetic data investigated herein, is supported by known and accepted evolutionary mechanisms, and is capable of producing testable hypotheses in independent fossil sequences. It provides a viable approach to understanding the fossil record, continuous throughout the microevolutionary and macroevolutionary levels.

Evolutionary biologists, and particularly paleoanthropologists, must continuously return to the basic paradigms set down in Darwinian natural selection and think about them in novel ways. Hypotheses generated within that context, and tested in the fossil record, may reveal that each lineage is the caldron of variability and species dynamics that catalyzes continuous evolution and speciation.

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