Mammalian Response to Cenozoic Climatic Change

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Key Words

population abundance, morphology, geographic range, functional
turnover, biotic turnover, immigration

Abstract

Multiple episodes of rapid and gradual climatic changes influenced the evo-
lution and ecology of mammalian species and communities throughout the
Cenozoic. Climatic change influenced the abundance, genetic diversity, mor-
phology, and geographic ranges of individual species. Within communities
these responses interacted to catalyze immigration, speciation, and extinc-
tion. Combined they affected long-term patterns of community stability,
functional turnover, biotic turnover, and diversity. Although the relative in-
fluence of climate on particular evolutionary processes is oft-debated, an
understanding of processes at the root of biotic change yields important in-
sights into the complexity of mammalian response. Ultimately, all responses
trace to events experienced by populations. However, many such processes
emerge as patterns above the species level, where shared life history traits
and evolutionary history allow us to generalize about mammalian response to
climatic change. These generalizations provide the greatest power to under-
stand and predict mammalian responses to current and future global change.

INTRODUCTION

Population: group of interbreeding individuals within a species

Abiotic: nonliving physical factors in the environment

mya: million years ago

As we grapple with the consequences of anthropogenic climatic change, understanding the biological response of species is one of our primary defenses in forestalling future biodiversity collapse. Anticipating that response, however, is hindered by three complicating issues: (*a*) We have little understanding about which species will be most sensitive, and what kinds of responses will be most common; (*b*) the full biological response to climatic change will operate over evolutionary time scales, but much of our knowledge of species dynamics has been gleaned from just a short time span—at best over a century, and often just a few years; and (*c*) extinction directly induced by habitat loss, habitat fragmentation, and overexploitation of populations is already proceeding at rates unparalleled in the Cenozoic (the past 65 million years), or perhaps the history of life. A longer-term perspective that encompasses how global warming interacts with species biology, extinction, and habitat loss is thus critical if we hope to understand how remaining species and communities will cope with ongoing global warming.

Organisms are obviously affected by their environment; what is less obvious is the extent to which the abiotic environment sculpts different hierarchical levels of life, and the influence of climate on interactions between processes at different levels. Parmesan et al. (2006) recently reviewed the influence of climatic change on extant species (including mammals) over annual to century timescales. Here, we complement this review by using the fossil record to illustrate how mammals reacted to climatic change through geologic time in order to establish the full spectrum of mammalian responses to climatic change and the extent to which the responses of the past century appear unusual.

SCOPE OF THE REVIEW

We focus on the relationship between climatic change and response of terrestrial mammals throughout the Cenozoic (see **Figure 1** for geologic time scale terminology), primarily because of their exceptionally good fossil record, but also because they provide a relevant exemplar system, in that they (*a*) already exhibit clear effects of anthropogenic climatic change (e.g., Beever et al. 2003, Schmidt & Jensen 2003); (*b*) fill important ecological roles within communities, such as, for example, predators, herbivores, earth engineers, seed dispersers, and scavengers; and (*c*) are taxonomically and morphologically diverse, occupying many habitats on all of today's continents (and oceans) except Antarctica. And even there, mammals were present until at least 30 mya (million years ago) (Pascual 2006).

The initial diversification of mammals occurred in the early Jurassic (Luo 2007), but we focus on the Cenozoic because we have yet to understand the full diversity of basal mammals. The Cenozoic witnessed several critical climatic events (Zachos et al. 2001), offering many opportunities to examine mammalian response to salient features of climatic change. However, several aspects of both the climate record and paleobiological systems deserve mention before assessing past mammalian responses to climatic change. First, the nature of paleontological data usually requires a correlational approach; thus, we make our conclusions as robust as possible by focusing on studies that explicitly investigate the links between climate and faunal change. Second, when possible we use local or regional climate proxies to assess paleobiological response rather than global proxies, recognizing that local paleoecological patterns are most accurately understood through the lens of regional climatic variation (although, of course, those regional changes typically are linked to a bigger global pattern). Third, we interpret studies keeping in mind that both marine and terrestrial paleoclimatic data often afford better temporal resolution than faunal data. This affects interpretations because the faunal data are often drawn from time periods where climate is variable
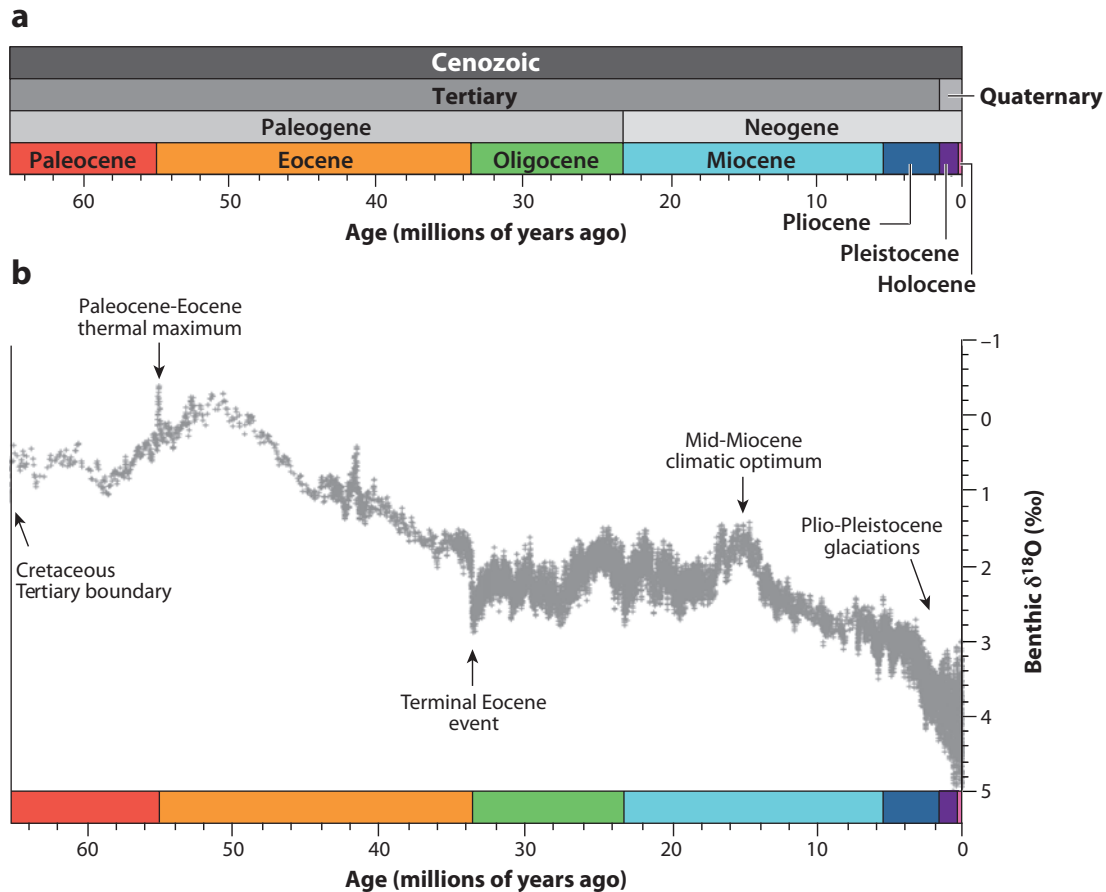
Figure 1

(*a*) Geologic time scale of the Cenozoic (the past 65 million years), indicating terminology used in this review. (*b*) Summary of important climatic events throughout the Cenozoic. Benthic $\delta^{18}O$ (‰) is a proxy for global ocean-water temperatures, with lower values corresponding to warmer temperatures. Important climatic events discussed in the section Biotic Turnover and Diversity and elsewhere are highlighted. Modified with permission from Zachos et al. 2001 and Jansen et al. 2007.

throughout the period, weakening the apparent signal of climate on biological response (Barnosky & Carrasco 2002, Stenseth & Mysterud 2005). Thus, longer, more time-averaged records are less likely to demonstrate rapid vertebrate response, meaning that, over longer time periods, short-term climatic fluctuations may not be recorded as discernible mammalian fossil responses at all.

A further challenge in assessing biotic response to climatic change is that we are seldom sure which aspects of climate drive an observed biotic response on almost any spatial or temporal scale (Humphries et al. 2004). This holds true not only for fossil taxa, but also for modern species (Araújo & Luoto 2007). Further, climatic drivers may be direct, influencing the physiology of individual animals, or indirect, in which climate affects, say, vegetation, which in turn acts as a filter through which the animals respond (Berteaux et al. 2006). Additionally, factors other than climate can influence every response we discuss here, from the effect of predation pressure or the presence of competitors on population abundance and morphology (Dayan et al. 2002, del Monte-Luna et al. 2004, Millien & Jaeger 2001) to the influence of biotic interactions on macroevolutionary

Macroevolution: evolutionary change at or above the species level

Functional turnover:
change in the ecological roles filled by mammalian community

processes (Jablonski 2008). Finally, the advent of phylogeographic and other genetic-based bio-geographic studies (Riddle et al. 2008) will be particularly helpful for revealing the importance of particular climatic events on lineage-specific evolution (e.g., Davis et al. 2008), potentially providing independent evidence for hypothesis-testing. Our purpose here is to present, to the fullest extent possible, the range of spatial and temporal scales at which particular responses to climatic change are investigated, highlighting recent examples from different continents, different taxa, different time periods, and using different approaches. Thus, we necessarily have neglected many classic as well as new and exciting studies in favor of highlighting the full spectrum of mammalian response to climatic change in our goal of providing a more global synthesis.

SCALES OF RESPONSE

Past reviews typically have defined scales of response to climatic change either spatially, temporally, or by discrete levels of the biological hierarchy (Jansson & Dynesius 2002, MacFadden 2000). Here, instead, we trace the effects of climate on particular biological processes and explore how they cascade through the continuum of time and space, starting at the levels of genes and individuals, and building up to multispecies communities and ecosystems (**Figure 2**). Our approach recognizes the mutual interdependence of ecology and evolution, highlights how biotic mechanisms interact to elicit change, and thereby attempts to synthesize the potential role of climate on biological processes.

Mammals exhibit many different responses to changes in their environments. An individual animal may, over the course of a day, move from sun to shade as a response to uncomfortable and stressful thermal conditions (e.g., Natori & Porter 2007); or co-occurring individuals may, in response to seasonal influences, change the timing of key life history events, such as mating, migration, or emergence from hibernation (Réale et al. 2003). Over yet longer time periods, population size can wax and wane in response to changing local climate, which in turn influences the amount of genetic diversity that will be transmitted from one generation to the next (Visser 2008). Scaling up, the effect of regional climatic impacts on populations is integrated across regions by population connectivity and gene flow. Over time these population processes, combined with the addition of genetic novelty, affect the prevalence of genes with adaptive potential for novel climates, which also is fodder for heritable changes within lineages (Garant et al. 2007). As connectivity between populations declines to zero, each population begins to diverge along independent evolutionary trajectories. Prolonged environmental trends may result in alteration within lineages, usually recognized in the fossil record by morphologic change (Benton & Pearson 2001) and population processes in isolation can result in speciation. Finally, extreme population size reduction can occur when species encounter climates for which they are not adapted, eventually resulting in extinction (Pimm et al. 1988).

Many responses usually regarded as macroevolution can be traced to processes occurring to individual populations, which is how we address these processes here. A large number of coincident local extinctions, speciations, and colonizations will become apparent as biotic turnover, or replacement in time and space of a large proportion of the community, and can also affect the overall role of the mammalian community within the ecosystem, here termed functional turnover. Turnover events can be very rapid, and are sufficiently profound that they are often used to designate boundaries of geologic time, for example, the North American Land Mammal Ages (Woodburne 2004).

We conceptualize the connections between each response to climatic change in **Figure 2** and discuss processes linking the responses in the context of our review. Our distinction between single-taxon responses and multitaxa responses is mostly a semantic one because many processes such as
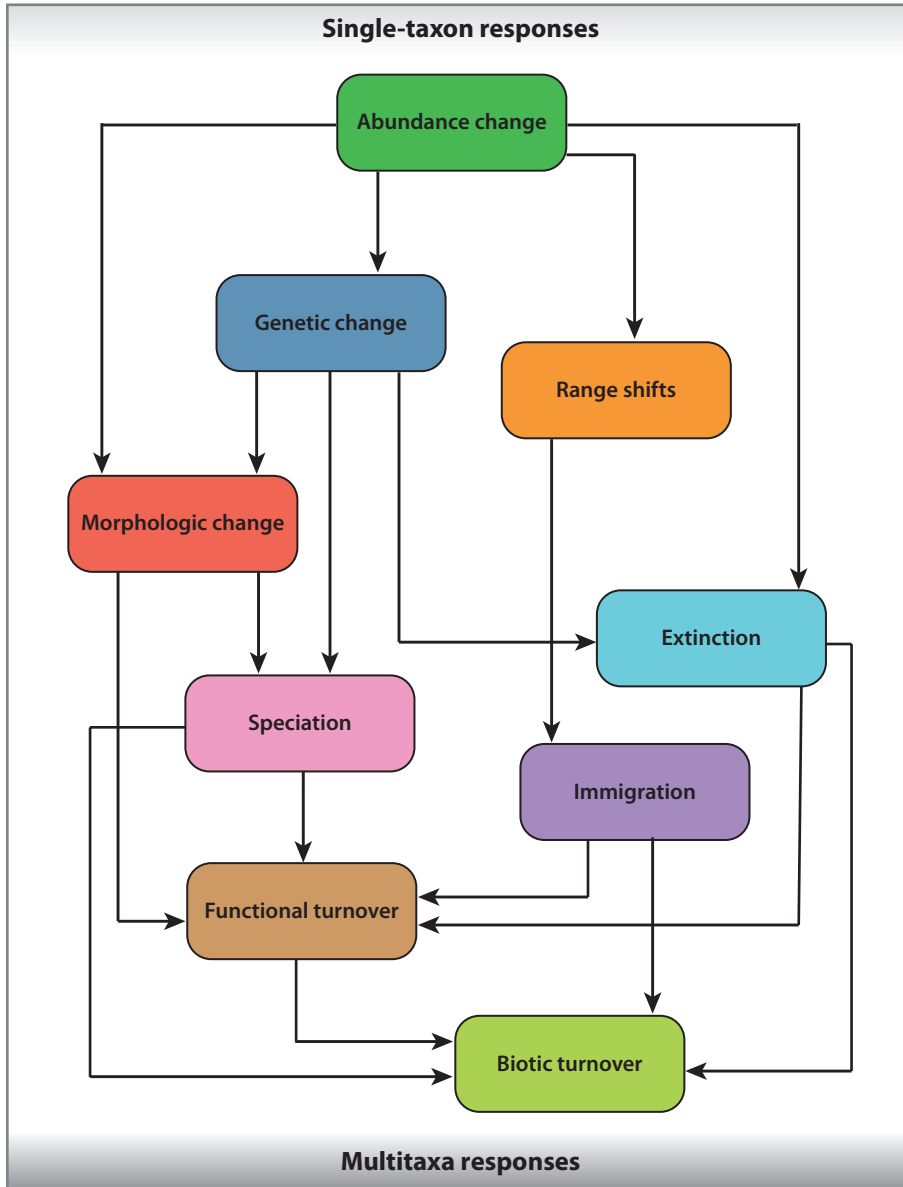
Figure 2

Connections between the various responses to climatic change seen in the fossil record and used in this review, grading from single-taxon responses such as changes in population abundance, genetic change, morphologic change, and range shift, up to responses often detected across multiple taxa such as large-scale immigration, speciation, extinction, and functional turnover, culminating in the largest scale response, biotic turnover. In each case, arrows denote processes that connect different responses. Colors in this figure correspond to the same processes and colors in **Figure 3**.

immigration, speciation, and extinction fundamentally occur within individual lineages, but are often investigated within the context of examining community-level change or biotic turnover. **Figure 3** highlights the temporal and spatial scale of mammalian responses documented in the particular studies we discuss.

## SINGLE-TAXON RESPONSES

Abundance Change

Changes in abundance are primarily the result of an animal's ability to survive in a particular place. Typically, aspects of the abiotic environment determine the population size or number of animals that can be supported within a given area (i.e., the carrying capacity) by governing the availability and suitability of the animal's preferred habitat (del Monte-Luna et al. 2004). A changing climate may influence population abundance by governing the overall landscape area available to species (geographic range), as well as determining whether individual populations are large or small (density or abundance), and how the populations are distributed within the total geographic range (patchy or continuous).

Population size changes are a first-order response of species to their environment, to which most of the other responses measured in the fossil record can be traced (**Figure 2**). For example, the distribution and abundance of populations (Lundberg et al. 2000) is important for determining the overall connectivity and resilience of the species, both in terms of population persistence via local extinction-recolonization dynamics (Hanski 1998) and in terms of the distribution and amount of genetic and morphologic diversity (Eckert et al. 2008). In general, maintenance of large population sizes with consistent connections between populations results in higher genetic and morphologic diversity, as well as increased likelihood of long-term persistence (Hadly 1996, Jernvall & Fortelius 2004, Pimm et al. 1988).

Abundance [or its proxy, site occupancy (Jernvall et al. 2004)] can be difficult to document, but some paleontological localities yield serially stacked layers, each comprising numerous individuals.

Figure 3

The spatial and temporal scales at which mammalian responses to climatic change have been documented and which are used in this review. Each icon corresponds to a group of mammals. The number to the right of each icon corresponds to the citation key, which follows. Note that some processes have been documented only at very specific times and scales (i.e., functional turnover), whereas others have been studied across broad scales of space and time (i.e., morphological change). Citation Key: Abundance Change 1. Barnosky et al. 2004; 2. Bobe & Behrensmeyer 2004; 3. Grayson 2006; 4. Hadly 1996, Hadly et al. 2004; 5. Guilday 1964; 6. Badgley et al. 2005; 7. Lindsay 1972; 8. Jernvall & Fortelius 2004. Genetic Change: 9. Hadly et al. 1998, 2004; 10. Chan et al. 2006; 11. Hofreiter et al. 2002, Valdiosera et al. 2008; 12. Shapiro et al. 2004. Morphological Change: 13. Schmidt & Jensen 2003; 14. Barnosky & Bell 2003, Guilday 1964; 15. Blois et al. 2008, Smith & Betancourt 1998; 16. Renaud et al. 2005; 17. Hadly et al. 1998; 18. Semprebon et al. 2004; 19. Van Valkenburgh 2007; 20. Wood et al. 2007; 21. Janis 2008; 22. Weaver & Steudel-Numbers 2005, Elton 2008. Range Shift: 23. Beever et al. 2003; 24. Parmesan 2006; 25. Guralnick 2007; 26. Graham et al. 1996, Lyons 2003; 27. Nogués-Bravo et al. 2008; 28. Stuart et al. 2004. Immigration: 29. Smith et al. 2006, Gingerich et al. 2008; 30. Stehli & Webb 1985, Pascual 2006, Flynn 2003; 31. Stewart & Disotell 1998, Bobe et al. 2002; 32. Métais et al. 2007; 33. Woodburne 2004. Speciation: 34. Barnosky 2001; 35. Barnosky 2005, Lister 2004; 36. van Dam et al. 2006; 37. Webb 1991; 38. Vrba 1995; 39. Bobe & Behrensmeyer 2004. Extinction: 40. Koch & Barnosky 2006; 41. Hopkins 2007; 42. Janis 1997, 2008; 43. Louys et al. 2007; 44. Nogués-Bravo et al. 2008; 45. Shapiro et al. 2004; 46. Vrba 1995; 47. Jernvall & Fortelius 2004, Liow et al. 2008. Functional Turnover: 48. Bown et al. 1994, Flynn et al. 2003, Gingerich 2006; 49. Janis 2008, Fortelius et al. 2002, Jernvall & Fortelius 2004; 50. Janis et al. 2004; 51. Jernvall et al. 1996; 52. Pascual 2006; 53. Croft 2001, MacFadden 2000; 54. Cook et al. 2000, Vizcaíno et al. 2006; 55. Hunt 2004. Biotic Turnover: 56. Badgley et al. 2005, Bobe & Behresmeyer 2004, Vrba 1995, Wesselman 1995; 57. Gingerich 2003; 58. Van Valkenburgh 1999; 59. Alroy 2000, Novacek 1999, Smith et al. 2004, Hooker 2000, Woodburne 2004; 60. Gheerbrant & Rage 2006, Pascual 2006; 61. Renaud et al. 2005.
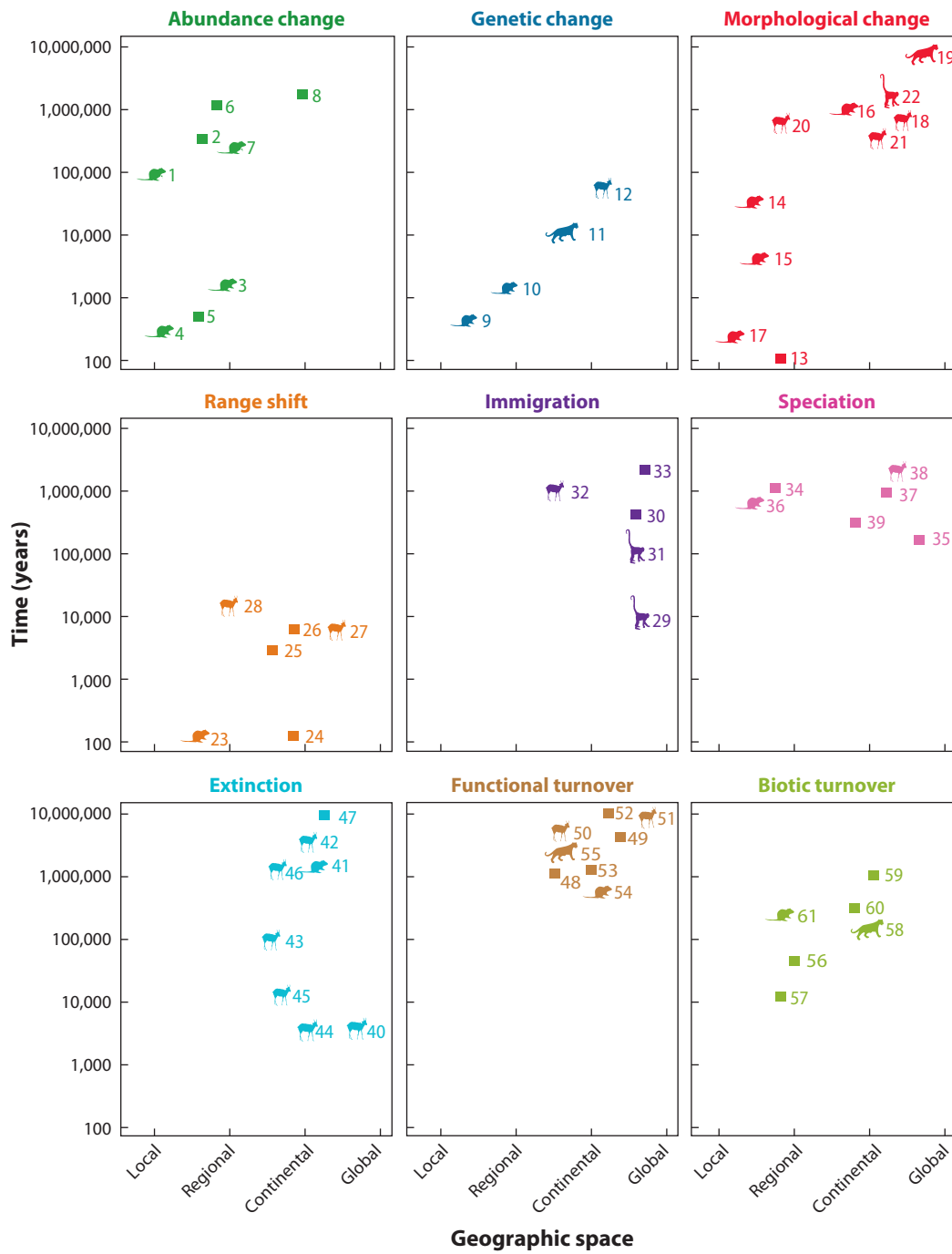
These deposits, common during the Quaternary, offer the opportunity to follow abundance changes over short geologic intervals. Investigations of changes in population abundance in the mammalian fossil record are one of the clearest demonstrations of the influence of changing environments on the biota of a region.

Life history can play a crucial role in interpreting abundance changes of certain species. For example, if local climatic changes result in cooler, wetter conditions, the abundance of species favoring mesic environments may increase as the percentage of their preferred habitat increases. This result was seen in North American voles (*Microtus* spp.) during mesic periods of the late Holocene, whereas the opposite pattern was found during the warmer and drier climates of the Medieval Climatic Optimum about 1000 years ago, when the abundance of the Uinta ground squirrel *(Spermophilus armatus)* increased. Species without strong habitat associations, such as deer mice (*Peromyscus maniculatus*) and the bushy-tailed wood rat (*Neotoma cinerea*), remained relatively constant during this same period (Hadly 1996). Similar examples are found in analyses of other Quaternary faunas (e.g., Barnosky et al. 2004, Grayson 2006, Guilday et al. 1964), and also sequences from deeper times in the Neogene (e.g., Badgley et al. 2005, Lindsay 1972) or the Cenozoic (MacFadden 2000). Thus, knowledge of life history and biology of species, as well as the habitat and climatic context, is crucial for interpreting, and predicting, the population abundance responses of species.

Additional power is gained when many records of local population abundances are summed across the landscape and through time, giving a regionally dynamic view of how environmental change affects species and the timing of population responses. In a regional study of late-Quaternary mammals of the Great Basin, Grayson (2006) demonstrated that several extant mesic-adapted species all underwent a reduction in their population sizes during the Pleistocene-Holocene transition, as their geographic ranges moved northward to their present limits.

Overall, fossil data provide good evidence of the links between population abundances and climate. The impacts of climate are seen mainly through changes to the overall amount of suitable habitat available to species, as well as the quality of the habitat, although biotic interactions may influence local abundance. Abundance often is correlated with other taxon attributes such as genetic diversity (Falconer & Mackay 1996), body size (Brown et al. 1996, Damuth 1981), and geographic range size (Brown 1996). Abundance increases and decreases also may be matched to genetic diversity using population genetic methods to reveal whether gene flow during periods of climatic change played a significant role in genetic diversity change (Hadly et al. 2004).

Genetic Change

Ancient DNA (aDNA) is emerging as an exciting area of research through which to interpret genetic responses to climatic change, at the level of individuals, populations, and species (e.g., Hadly et al. 2004, Hofreiter et al. 2002). The promise of ancient genetic data is that it produces direct evidence of past genetic variation and is a powerful tool for assessing the genetic signatures of climatic change through time, especially at the exact temporal scale (hundreds of years) over which future global change will affect modern species (Flessa & Jackson 2005).

However, measuring population-level genetic change directly from the fossil record is challenging even with extant representatives of modern species; only in rare cases has it been possible with extinct species. In part, this is due to the fact that degradation of DNA occurs immediately after death and even under optimal conditions almost no animal fossils preserve DNA older than 100,000 years (Willerslev & Cooper 2005). However, high-throughput and novel sequencing methods should facilitate even greater application of aDNA studies in the near future (Hofreiter 2008).

Changing climates can modify the selective pressures on species, thus altering frequencies of adaptive genes and overall levels of genetic diversity, and through changes to population abundance and density, can also influence evolutionary trajectories by mechanisms such as random drift. Climatic change can additionally increase or decrease gene flow by changing population connectivity (e.g., Hadly et al. 2004, Valdiosera et al. 2008), and theoretical models now exist to assess the effects of these processes on genetic diversity. These models have shown that the addition of ancient temporal data can greatly increase the probability of revealing the correct evolutionary history of populations and species over modern data alone (Chan et al. 2006, Ramakrishnan et al. 2005).

Some ancient genetic studies have addressed specifically the role that climatic change plays in past population movements (gene flow) in mammals [e.g., brown bears (Barnes et al. 2002), cave bears (Orlando et al. 2002, Hofrieter et al. 2007), foxes (Dalén et al. 2007), gophers (Hadly et al. 1998), horses (Orlando et al. 2006), squirrels (van Tuinen et al. 2008), and voles (Hadly et al. 2004)]. Ancient DNA studies also have tracked genetic diversity associated with climatic change before and during population size change [e.g., bison (Shapiro et al. 2004), voles and gophers (Hadly et al. 2004), tuco-tucos (Chan et al. 2006), brown bears (Barnes et al. 2002, Calvignac et al. 2008, Valdiosera et al. 2008), wolves and dogs (Leonard et al. 2002), and mammoths (Barnes et al. 2007)].

In general, such studies have shown that climate influences both gene flow and population size, but differently depending on the species involved. Study of genetic diversity through time is in its infancy, with limited theoretical or empirical generalizations available. However, insights from population genetic theory about population size and gene flow are already proving valuable (Anderson et al. 2005, Chan et al. 2006, Ramakrishnan & Hadly 2009).

Morphologic Change

Morphologic change is one of the most commonly documented responses to climate in the fossil record of mammals for several reasons. First, the bones and teeth of mammals conveniently preserve important information about two traits—locomotion and diet—that play an important role in the evolutionary history of mammals. Additionally, morphology is a common route through which both genetic and nongenetic forces are expressed. Morphologic response may be due to the physiology of the organism, in particular how energy is funneled to tissues, which often is expressed as growth or body size change (Rezende et al. 2004). For example, an animal may show different phenotypes based on the environment it experiences (i.e., ecophenotypes) (Réale et al. 2003). This type of morphologic response is not heritable, but may be recognized as a body-size trend within a population. The phenotype is also a primary target for the force of selection and may show prolonged, parallel, and repetitive trends in size and/or shape that are underlain by genetic change and thus, are heritable. These two responses (ecophenotypes versus heritable variation) both may be caused by climatic change (Réale et al. 2003), and both have been detected in the fossil record.

Climate may shape morphological characteristics of mammals through both direct and indirect processes. For example, many studies infer the direct selective pressure of temperature on body size due to physiology, often resulting in a pattern known as Bergmann's Rule (e.g., Ashton et al. 2000). Because the surface area:volume ratio of an individual is negatively correlated with size, larger size may help prevent heat from escaping across body surfaces (advantageous in colder climates); conversely, smaller size may facilitate heat dissipation (advantageous in warm climates) (but see Ashton et al. 2000). The relationship between temperature and body size of individual species has been exploited as an independent proxy of paleoclimate (Klein & Scott 1989, Smith & Betancourt 1998). Significantly, most of these examples are drawn from late-Pleistocene or Holocene populations, where the lineage studied still persists on the modern landscape and

Phenotype:
observable characteristics of an individual, governed by both genetic and environmental factors

generalizations about the relationship between body size and climate are less problematic. For example, the North American woodrat (*Neotoma cinerea*) exhibits a decrease in size linked to temperature change during the late Pleistocene through the Holocene (Smith & Betancourt 1998). Guilday et al. (1964) documented that the change in size of 13 fossil species through the Pleistocene-Holocene transition was correctly predicted based on the modern relationship between body size and latitude, which is generally correlated with temperature.

However, climate variables other than temperature also affect body size (Baumgardner & Kennedy 1993, Rezende et al. 2004). For example, seasonality may have influenced late Pleistocene gigantism (Guthrie 1984). Also, winter length can determine body size of populations by affecting the fasting endurance of those individuals that do not migrate to warmer climates (e.g., Ashton et al. 2000). Precipitation is particularly important but often underemphasized; research on both modern and fossil mammals shows that body size may be more strongly influenced by precipitation and primary productivity, both alone and in combination with temperature, than by temperature alone (Blois et al. 2008, Yom-Tov & Geffen 2006).

In general, the influence of precipitation (and also seasonality) on body size and shape is linked indirectly through controls on vegetation and primary productivity. For example, studies of gophers have documented that variation in nutritional quality, which itself is governed by other environmental factors (Patton & Brylski 1987), can induce plastic changes in body-size. Using both ecophenotypically labile and population-specific morphologic traits, Hadly et al. (1998) documented some phenotypic, but not genetic, body size fluctuations in fossil pocket gophers from the northern Rocky Mountains of North America. Additionally, tooth shape changed, apparently in response to increasing aridity, in several different taxa and at several different drying events: for example, in Mio-Pleistocene murine rodents in North Africa (Renaud et al. 1999); in many large herbivores in North and South America (MacFadden 2000); and in Pleistocene voles in North America (Barnosky & Bell 2003). These examples also demonstrate that it is possible to detect when adaptive genetic changes have occurred in populations through morphology because the underlying developmental controls of tooth formation have a genetic basis, as opposed to being sculpted by the environment directly (Kavanagh et al. 2007).

In some cases, there can be a significant time-lag between the climate change and morphologic response. For example, changes in skull morphology and dental microwear and mesowear in the extinct ruminant artiodactyl group Dromomerycidae suggested an adjustment in diet during the late Miocene to Pliocene aridification and cooling of the North American High Plains; however, skull morphology apparently lagged behind the dietary shift (Semprebon et al. 2004). Isotope studies reveal that dietary changes also are more labile than morphologic changes (Feranec 2007), an insight that may explain the lack of temporal synchronicity between changes to tooth shape and wear (Janis 2008, Joomun et al. 2008). Similar lags or decoupling between climatic change and various aspects of morphology are evident in the *Ectocion* lineage, which shows stasis in molar shape even with a dramatic reduction in body size ($\sim-50\%$) at the severe Paleocene-Eocene Thermal Maximum ~55 mya (Wood et al. 2007). Indeed, there is no reason to suspect that climate should cause all morphological traits to change in concert, even in a given suite of related characters. Thus, an understanding of which phenotypic traits confer advantages in particular environments is an important future research direction.

Other aspects of the mammalian skeleton may also respond indirectly to climatic change (Dayan et al. 2002), notably limb morphology (Janis 2008). Climate and energy efficiency for mobility were both implicated in sculpting the limb proportions of Neandertals in the Upper Paleolithic of Europe (Weaver & Steudel-Numbers 2005). Lengthening of limbs for increased cursoriality, which constitutes both size and shape change in response to more open environments, has occurred in other mammals as well (Elton 2008, Janis 2008, MacFadden 2000).

Cursoriality: running ability

It is also important to recognize that each species' morphological response to a given climatic change is individualistic (e.g., Renaud et al. 2005, Wood et al. 2007) and depends on its own natural history and the nature of the climatic change. For this reason, it is difficult to generalize about size and/or shape change across all mammals; however, analyses rooted in life histories have helped to identify and generalize the spectrum of responses possible with mammals. For example, we expect increasing body size to be more common during cooler, more arid intervals, and decreasing size to be more common across species during warmer, often wetter periods. In addition, species of particular sizes, proportions, and modes of life are often associated with particular habitats (Liow et al. 2008), such as smaller frugivores and tropical forests or large, cursorial mammals and open country, features which have been exploited for paleocommunity reconstructions (see Multitaxon Responses, below).

Range Shifts

The geographic distribution limits of many species are set primarily by environmental parameters (Brown et al. 1996). Thus, as climate changes, the range of a species is expected to change in accordance with their individual tolerances (Graham et al. 1996). A variety of specific climatic drivers (and sometimes interactions between individual drivers) have been postulated to drive range shifts, including orbital variations (Jansson & Dynesius 2002), temperature (Root 1988), humidity (Eronen & Rook 2004), and seasonality (Graham & Mead 1987). Species interactions also are clearly important is some cases (Kaufman 1995).

Past changes in the geographic ranges of mammals have been particularly well documented in North America and Europe due to their relatively good fossil records, an abundance of paleontologists, and a focused effort to create spatially explicit fossil locality databases (Fortelius 2008, Graham 1996). Species responded individualistically to climatic changes (e.g., Graham et al. 1996), with examples of ranges shifting in all directions and at varying rates. However, several important patterns have emerged from aggregating individual responses. For example, in North America, northern range limits shifted larger distances than southern limits, on average, between preglacial to glacial times and glacial to Holocene times (Lyons 2003), although differential responses of mountain-dwelling and flatland mammals may have obscured southern range limit trends (Guralnick 2007).

Circumstances of geography also may ameliorate the direct influence of climate (Bruzgul & Hadly 2007, Moreno Bofarull et al. 2008). Most analyzed North American mammals shifted their ranges within geographical provinces at the end of the Pleistocene, with extralimital records generally found in only one different province, rather than several. Thus, even though species ranges shifted substantially at the end of the Pleistocene, the basic relationship between species and habitats remained coherent (see sidebar, Community Stability). This observation is key to interpreting details of range changes, where one common assumption is that the environmental niche of a species is relatively stable. For example, several recent studies have surmised that decreasing geographic extent and population size may have led to increased susceptibility of some species to extinction by human-hunting (Nogués-Bravo et al. 2008). Thus, climatically-driven changes to habitat can interact with abundance, range size and distribution, and biotic factors to produce many of the patterns observed in the fossil record (e.g., Grayson & Delpech 2005, Stuart et al. 2004).

Not all species will exhibit changes to their geographic range during periods of climatic change. Further, the probability of detecting change is higher at the periphery of the range than at its core, which often is not appreciated in documentation of fossil presence–absence data, and underscores the value of georeferenced paleontological data. There is a need to explicitly quantify the rate of

COMMUNITY STABILITY

Mammalian communities may remain remarkably stable in the face of climatic change. For example, the structure of European mammalian communities of the past 20 million years remained constant despite continuous turnover of the dominant herbivores (Jernvall & Fortelius 2004). Thus, even though the common herbivores were changing and individual species showed adaptive responses to the varying environment, the trophic structure of the community remained the same. Similar conclusions were drawn in a study of mammalian responses to 500,000 years of climatic change in the late Pleistocene of Australia (Prideaux et al. 2007) and over the past 1,000,000 years in North America (McGill et al. 2005). Although relative abundances of mammals fluctuated, the dominant species of the montane mammal community did not change; rare species remained rare and common species remained common, in spite of many glacial-interglacial cycles (McGill et al. 2005). These studies are compelling because they suggest maintenance of trophic structure in spite of significant environmental change (Martinez-Meyer et al. 2004); however, they also support the sensitivity of individual species to climate. A more detailed unraveling of the predictability and spectrum of mammalian response given these insights is critical.

range change versus the rate of climatic change, as well as to consider empirically the causes and consequences of differential dynamics on trailing and leading edges of range shifts (Eckert et al. 2008, Ghalambor et al. 2007).

MULTITAXON RESPONSES

The full impacts of single-taxon responses often aggregate and thereby become evident at the community level. In the following sections, we consider whether such aggregated responses within and between continents reflect responses to climate change; in this respect, we interpret the results of many different natural experiments in which climate changed at various times during the past 65 million years. We investigate continental faunal exchange via immigration, whether climate is linked to increased probability of speciation and extinction, whether evolution in multiple lineages results in functional turnover, and the role of climate in biotic turnovers.

Immigration

Global climatic change may stimulate animal movements by opening or closing corridors of suitable habitat within or among continents (Vrba 1992). Intercontinental immigration events may result from processes such as rafting or movement across land bridges. Land bridges were often exposed during the Cenozoic due to climatic cooling events when increased glaciation resulted in lower sea levels (e.g., Voris 2000). These intercontinental land bridges merge previously independently evolved taxa into new communities, leading to dynamic shifts in community structure that may cause an increase in speciation, extinction and/or functional turnover, or may simply result in an overall increase in continental richness (Vermeij 1991). Additionally, the global climatic changes that influenced the physical connection between continents altered existing habitats, creating novel environments for both native and immigrant species.

Examples of land bridges that resulted from climatic change include the North Atlantic land bridge (Smith et al. 2006), which may have facilitated dispersal of primates between North America and Europe near the Paleocene-Eocene Thermal Maximum (Smith et al. 2006), and numerous interisland and intercontinental connections in southeast Asia (Voris 2000) at various times during the Cenozoic (Métais et al. 2007). Old World continental connections, particularly the relative

roles of exchanges between Africa, Europe, and Asia, have been intensively investigated due to the focus on migration and evolution of humans (Stewart & Disotell 1998). Additionally, migration into Africa by non-Afrotherian clades are an important but underappreciated aspect of faunal change (e.g., Matthee & Davis 2001). Study of climate as well as intercontinental connections in Eurasia supports the primacy of climate in directly determining mammalian community dynamics in the latest Cenozoic. One of the best-known connections between continents is the Beringian land bridge that periodically emerged between eastern Asia and North America throughout the Cenozoic, facilitating exchange of many different mammals in both directions. These immigration events often help define Land Mammal Ages or Zones (e.g., Woodburne 2004). All of these examples provide strong evidence that climatic change triggers intercontinental dispersal, given that there is coincident faunal community turnover, independent evidence of climatic change (such as from isotopic data or vegetation), and changes in community structure indicating productivity shifts.

However, not all intercontinental connections directly result from the effects of climate. For example, the emergence of the Panamanian land bridge was catalyzed by plate tectonics and fully connected North and South America ∼3 mya (Stehli & Webb 1985). The intermingling of these two faunas resulted in the Great American Biotic Interchange (GABI), a cascade of events leading to faunal turnover in South America. Whereas the physical connection was facilitated by tectonics, climatic cooling during and subsequent to the event catalyzed the transition from continuous tropical forest environments to a mosaic of grassland habitats. Thus, during the exchange, dominance of movement was south by North American grassland specialists, whereas northerly movement of tropical forms was limited. The GABI also highlights that land bridge connections, whether or not they are facilitated by global climatic change, may simply introduce animals to environments in which they previously could have survived but to which they could not disperse (Thuiller 2007), and underscores that the relative roles of immigration and climate may not always be easy to untangle.

GABI: Great American Biotic Interchange

Speciation

Climatic change may contribute to cladogenic (splitting) speciation by isolating populations within the geographic range of species (Gould & Eldredge 1977). Prolonged environmental change may also contribute to anagenesis, recognized by up to millions of years of unidirectional morphological change in the fossil record (Simpson 1951). Proposed mechanisms that invoke climate change, such as the turnover-pulse hypothesis (Vrba 1993), rely on associations between species and particular habitats. Thus, as habitats change and at times become fragmented due to climatic change, populations are hypothesized to follow independent evolutionary trajectories.

It is easy to envision that large changes in environment will lead to simultaneous cladogenic events across taxa, but support for these types of events are lacking for some of the best known environmental events such as those experienced during the Plio-Pleistocene glacial-interglacial cycles. Throughout the 1.8 million years of the Quaternary, speciation rates are not elevated above background levels in North American mammals, as would be predicted if climate significantly impacted species diversity through macroevolution (Barnosky 2005, Barnosky et al. 2003). Neither did a detailed analysis of African faunal change support the turnover-pulse hypothesis and reveal enhanced speciation (Bobe & Behrensmeyer 2004). Instead, most of the community changes were attributed to population-level change, immigration, and extinction due to repeated cooling and drying events (Bobe & Behrensmeyer 2004). However, the two million years of the Quaternary also span less time than may be adequate to generate appreciable speciation in mammals. The lifetime of mammalian species through the Cenozoic ranges between 1 and 16 million years as

calculated from the fossil record (Alroy 2000, Liow et al. 2008). Mammalian molecular data show divergences between extant sister species that are roughly in agreement with fossil estimates, on the order of 3 to 10 million years (Avise et al. 1998, Baker & Bradley 2006). Lister (2004) contended that turnover (i.e., originations and extinctions) was greater in the Quaternary than for similar time units within the Miocene in Italy, a contrasting result that may be due to the more constrained spatial scale and particular location at which the study took place. Further, systematic variation in evolutionary rates (with or without the stimulation of climatic change) may also be accounted for by species assemblages of similar age, trophic category, body size, lineage, or life history (e.g., Liow 2008, van Dam et al. 2006).

Climate-induced speciation events, however, are clearly evident over longer time periods prior to the Quaternary. A strong correlation was found in central Spain for a between-species turnover of Miocene rodents (origination plus extinction) and orbitally forced climate oscillations with periods of 1.2 and 2.4 million years (van Dam et al. 2006). Webb (1991) argued for elevated rates of speciation in the North American mammals that moved to South America during the GABI due to habitat and lineage-specific factors that favored their migration in the first place. Recent molecular support for this insight is provided by the relative rates of diversification in murine rodents in North and South America, where the South American lineages experienced enhanced speciation relative to North American lineages over the same time (Steppan et al. 2004).

Some argue for a relatively constant dynamic between speciation and extinction at one million year time increments (Alroy et al. 2000), regardless of climate. One interpretation is that although climatic change acts over millennia, the dynamics of speciation may occur over millions of years, thus obscuring the signal of climate. An alternative interpretation is that climate does not have a proportionately greater influence on speciation and extinction rates than do biotic interactions such as competition or predation (Alroy et al. 2000), although particular evidence for competition as a macroevolutionary driver is lacking (but see Araújo & Luoto 2007).

In sum, whereas it is not always clear what the role of climate is in stimulating evolution at the largest geographic scales and at temporal scales shorter than a typical mammalian species duration, in biotic provinces such as parts of Africa, South America, North America, and Eurasia there seems to be compelling evidence that evolutionary changes accompanied climate changes over several millions of years, particularly in lineages tied to grassland expansion such as the Equidae during the Miocene (e.g., MacFadden 2000) (see also Functional Turnover and Biotic Turnover and Species Diversity, below). A more resolved understanding of the role that climate plays in generating evolutionary novelty is critical for predicting future diversity changes (Dirzo & Raven 2003, Jansson & Dynesius 2002).

Extinction

Much neontological and paleontological literature has analyzed the factors associated with extinction risk (Ceballos & Ehrlich 2002, Jernvall & Fortelius 2004). These factors include intrinsic traits such as fecundity, body size, degree of specialization, rarity, and generation time and extrinsic traits such as anthropogenic habitat reduction, human hunting, stochastic effects, and climatic change. When extinction occurs synchronously across many different lineages, primarily extrinsic factors are implicated, as in the case of the event that caused the extinction of the dinosaurs at the end of the Cretaceous (Jablonski 1989). However, in cases of single lineage extinction events, intrinsic and extrinsic factors may work together. Climatic change may cause, for example, vicariant separation of geographic distributions leading to small, isolated populations and a higher probability of extinction, a process recognized in relative rates of turnover in African antelopes (Vrba 1995). Species that are highly specialized to particular climatic regimes and/or habitat types will be

more vulnerable to extinction in this case than less specialized species, but with climatic changes of larger magnitude, these same mechanisms may also affect less specialized species (Ceballos & Ehrlich 2002).

Some paleontological studies have teased apart the influence of various extinction risk factors. For example, Liow et al. (2008) found that large-bodied mammals were more likely to experience higher extinction (and origination) rates, and thus, had shorter species durations, than small mammals. The authors attributed this tendency to the inability of large mammals to adopt environmental buffering strategies. Janis (1997) found that ungulates experienced extinction correlated with cooling at the end of the Eocene but that not all types of ungulates experienced extinction evenly. Archaic ungulates and ungulate-like mammals experienced extinction during the moderate cooling in the middle Eocene, whereas in the lineages leading to modern ungulates, elevated extinction rates were delayed until the late Eocene. Hopkins (2007) suggested that neither climate nor competitive interactions were strongly correlated with extensive diversity fluctuations in aplodontid rodents, but that different climatic factors may have indirectly impacted both diversification and extinction. Diversification was concordant with the timing of the Middle Miocene Climatic Optimum between 14 and 17.5 mya (at the same time many other clades experienced significant changes; see Biotic Turnover, below) and lineage decline was linked to the spread of C-4 dominated grasslands at the end of the Miocene.

Much discussion has focused on the causes of the end-Pleistocene megafaunal extinction (reviewed in Koch & Barnosky 2006). Climate change seems to have played a role in several places, although human impacts are undeniable as a major factor, especially in places like North America and Australia. New techniques and data allow for a growing appreciation of the interactions between multiple drivers (Nogués-Bravo et al. 2008, Shapiro et al. 2004). For example, in southeast Asia humans and megafauna coexisted for a long period, and the persistence of megafauna for thousands of years despite indirect indications of human hunting argues humans weren't the sole cause of megafaunal extinction (Louys et al. 2007). Rather, there appears to have been a synergy of human impacts with climate change manifested as a more variable and/or drier climate developing over the past 200,000 years, with sea level increase significantly decreasing the area of southeast Asian land masses (Voris 2000).

Some of the most tangible evidence of global human impact today, including the effects of climatic change, has been measured in increased rates of extinction (Ceballos & Ehrlich 2002), yet data from the fossil record specifically linking climate and extinction are few, with notable exceptions such as those cited above. Additionally, few studies of the fossil record document how population decline and shrinking geographic ranges are linked with eventual species extinction (but see Grayson 2006, Nogués-Bravo et al. 2008), although climate clearly plays a role. The synthesis of population size, niche modeling, climate modeling, genetic data, body size decline, and disease risk, as well as improved estimates on the timing and intensity of human disturbance, are needed to help us parse the relative roles of these factors in late Pleistocene extinctions and others.

Functional Turnover

The integration of evolutionary and ecological processes induced by climatic change can create a community with novel functional traits—termed functional turnover—even while holding the number of species constant. Among community traits that signal functional turnover are changes in body size distributions (which reflect alterations in energy flow through an ecosystem), changes in dentition, such as the prevalence of hypsodonty, or particularly high-crowned, enamel-covered teeth (an indicator of the plant-animal dynamic), isotopic signatures of habitat utilization

Niche: relational position of a species in its biotic and abiotic environment

Hypsodont: high-crowned dentition, thought to evolve in response to increased wear on teeth

(how animals use the landscape), and overall species diversity (amount of primary productivity available).

Analyses of the body size distribution of South American herbivores through the Cenozoic suggested that smaller, forest species gave rise to larger, open grassland species, mostly consistent with other paleoclimatic data, but earlier than indicated from analyses based solely on morphology of individual species (Croft 2001). Additionally, within lineages of early Eocene condylarths and primates from Bighorn Basin, Wyoming, relatively small-bodied forms appeared in warmer times and relatively larger forms in cooler periods (Bown et al. 1994). The Bighorn Basin body size shifts were attributed to episodes of climatically-induced immigration and differential extinction by particular taxa rather than elevated speciation rates.

Dentition has been particularly useful in recognizing fundamental shifts in the structure of communities. For example, trends toward increasing hypsodonty have been well documented in faunas worldwide (South America: Flynn et al. 2003, Pascual 2006, Eurasia: Fortelius et al. 2002, Jernvall & Fortelius 2002; North America: Janis et al. 2004). Thus, hypsodonty is a world-wide signal of vegetation change, and is usually associated with cooling and aridity, although questions remain about the temporal synchrony of grassland expansion and hypsodonty (Strömberg 2006), as well as the influence of other factors such as siliceous abrasives from volcanic ash due to mountain-building (Kay et al. 1999). Climatically-induced functional turnover also is indicated by increasing disparity of ungulate molar types during the Paleocene through Eocene (Jernvall et al. 1996). High temperatures and, presumably, high productivity resulted in more ungulate niches during the Paleocene-Eocene transition compared to the narrowed niche space of the subsequent, cooler Miocene. Thus, although climate induced an increase in the diversity of hypsodont taxa, morphological disparity across all ungulates actually declined, suggesting that the Miocene was a period of increased ecological competition.

Morphological features related to locomotion also have changed in response to climatic change. A classic example is limb evolution in ungulates, with a transition from a small, delicate, forest-dwelling fauna of the early Miocene to a cursorial, open-environment fauna, corresponding with the transition from browser- to grazer-dominated communities and the opening of environments in the mid-Miocene (Janis 2008). In this case, the link with climate is a second-order one through increasingly open vegetation and potentially through coevolution of predators. An association between dry and open environments of the early to middle Miocene and morphology and diversity associated with digging adaptations has been hypothesized for armadillos in South America (Vizcaíno et al. 2006). However, a global study of several distantly related fossil subterranean rodent families did not find synchronous diversification within the subterranean niche. Instead, families radiated from the Oligocene through the Plio-Pleistocene (Cook et al. 2000), suggesting that different fossorial lineages are uniquely affected by climate, key climatic events influencing diversification are more regional than global for this group, or unknown factors are influencing diversification.

At the largest temporal and geographic scales, mammalian communities have undergone significant changes in structure and function associated with global climatic change of the Cenozoic. For example, much of North America during the Paleogene was dominated by subtropical forests replete with frugivores, primates, and small herbivores (e.g., Gingerich 2006). The Miocene witnessed a transformation into swaths of open country with larger grazing herbivores and predatory mammals (Hunt 2004, MacFadden 2000). Today, many of the same areas are covered with arid shrub-grassland and desert. Modern studies of mammalian community structure and beta diversity are yielding insights about the underlying controls on functional turnover such as productivity, lineage effects, and the role of climate in fossil systems (Adler & Levine 2007). Synthesis of these fields with paleontology is a particularly exciting avenue of future research.
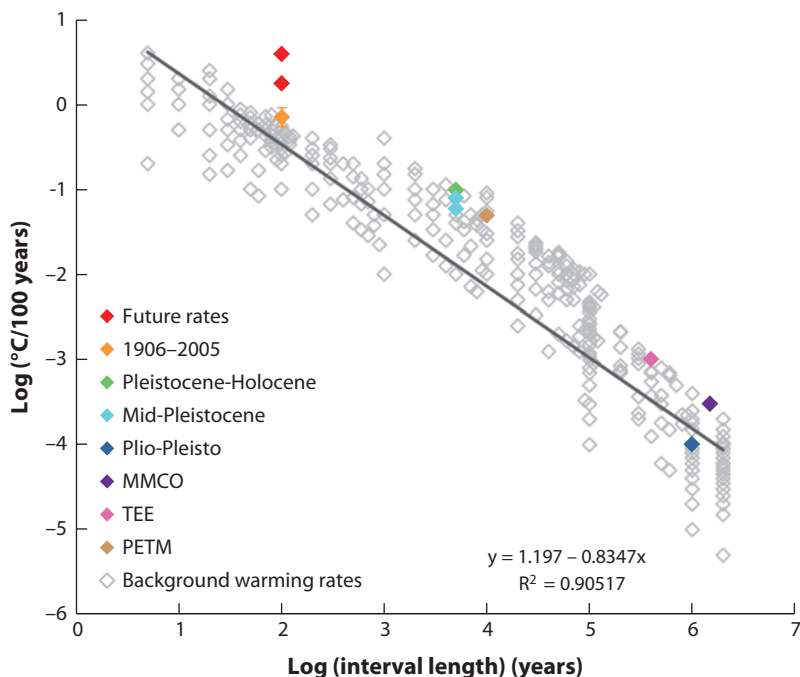
Coevolution:
evolution of species in response to change in other, interacting species

Beta diversity:
change in species composition from one community to another in geographic space, deemed turnover through time

Figure 4

Per-100-year temperature-change rates for different intervals throughout the Cenozoic, on a log-log scale.
The best-fit line is shown. All rates plotted are rates of warming, except for the terminal eocene event (TEE),
which is rate of cooling. The 1906–2005 per-100-year warming rate is estimated at 0.74 ± 0.18. Future
rates are based on estimates of future temperature in 2090–2099 for different emissions scenarios. The low
estimate corresponds to the B1 emissions scenario, and the high estimate corresponds to the A1F1 emissions
scenario. Past and future 100-year data from the Intergovernmental Panel on Climate Change 2007
assessment (Solomon et al. 2007a). TEE data from Zachos et al. 2001. Paleocene-Eocene thermal maximum
(PETM) data from Zachos et al. 2008. All other data are from the upper graph of **Figure 2** in Barnosky et al.
2003. MMCO, mid-Miocene climatic optimum. Modified with permission from Barnosky et al. 2003.

Biotic Turnover and Species Diversity

Biotic turnover results from processes (abundance change, immigration, speciation, and extinc-
tion) that ultimately trace back to alteration of the abiotic environment causing simultaneous
response in multiple species. Climates changed at various rates (**Figure 4**) across the Cenozoic,
but overwhelming evidence that climate paces biotic turnover is lacking across this time period
(Alroy et al. 2000). In general, the longer period over which climatic change is measured, the
lower the magnitude of change detected, in part because only mean climatic signal is recorded
(Barnosky et al. 2003). Thus, the signal of biotic turnover, usually measured over longer temporal
scales than many other biotic responses (**Figure 3**), may be expected to be weak. Clearly, though,
climate has profoundly affected biotic turnover at particular times and places. A brief overview of
the history and themes in mammalian evolution follows, where we highlight major biotic turnover
events (see **Figure 1** for the climatic context corresponding to each event).

By the end of the Cretaceous, several extinct lineages and all three modern mammalian
subclasses (monotremes, marsupials, and placentals) were present (Alroy 2000, Novacek 1999).
Although fossil data are sparse, molecular evidence suggests that representatives of all modern
mammalian orders were also present (Bininda-Emonds et al. 2007). Paleontological specimens

show that pre-Tertiary mammals were mostly small, on average approximately 200 grams (Smith et al. 2004), and most were insectivorous or frugivorous (Hooker 2000).

Cretaceous-Tertiary (K-T) turnover event. The first mammalian turnover recorded in the fossil record occurred at the Cretaceous-Tertiary boundary. Although this event was not caused by climate change per se, it is associated with changing climates and changing sea-levels, perhaps leading to an increase in intercontinental dispersals and subsequent radiations in Mammalia (Novacek 1999). The K-T boundary, marked most famously by the extinction of dinosaurs, also witnessed a dramatic turnover in mammalian communities where superposed strata exist. In Montana, 79% of the Cretaceous mammals went extinct, and were replaced by a community dominated by 73% novel mammals (Hooker 2000). This initiated an important trend throughout the Cenozoic, diversification in body size and diet; mammals became orders of magnitude smaller and larger than their Cretaceous ancestors, eventually specializing in both plant and animal consumption and occupying terrestrial, arboreal, subterranean, and aquatic habitats.

Paleocene-Eocene turnover event (PETM). Approximately 55 mya, the first major turnover event within the Cenozoic affected all northern continents and potentially Africa (Gheerbrant & Rage 2006, Novacek 1999, Woodburne 2004), although it is unclear how faunas in other regions responded due to their poor Paleogene fossil record. First occurrences of major clades including perissodactyls, artiodactyls, primates, and bats characterize this period for both North America and Europe. Global climate experienced a warming trend, punctuated by an abrupt and pronounced increase in temperature, the Paleocene-Eocene Thermal Maximum (**Figure 1**, Zachos et al. 2008). The PETM was the most pronounced warming of the Cenozoic, with the lowest equator-to-pole temperature gradient of the past 55 million years (Moran et al. 2006). The subsequent early Eocene experienced the greatest extent of tropical and subtropical forests ever achieved, with the most homogenous Holoarctic faunas of the entire Cenozoic (Woodburne 2004).

Terminal Eocene Event. Global mammalian faunal turnover involved climatic cooling at the Eocene-Oligocene boundary, known as the Terminal Eocene Event (TEE). Characterized by rapid cooling brought about by deep circum-Antarctic circulation (Zachos et al. 2008) and development of the first polar ice caps, the TEE saw a decline in sea level and significant changes in the faunas of Europe, Asia, and the Americas (Novacek 1999, Pascual 2006). Most of the turnover involved the loss of extremely large browsers such as brontotheres and the exchange and homogenization of several groups of smaller mammals. It also was marked by turnover in the carnivoran guild of mammals (Van Valkenburgh 1999). In Europe, this event, known as the Grande Coupure, resulted in the extinction of 82% of the placental mammals in places and is correlated with an increase in latitudinal temperature gradients (Hooker 2000).

Mid-Miocene Climatic Optimum. The subsequent biotic turnover event was marked by climatic change during the middle Miocene (**Figure 1**). Biotic turnover at the Mid-Miocene Climatic Optimum (MMCO), although documented as peaking at slightly different times on some continents, was tied to expansion of temperate grasslands, which, in turn, were initiated by global cooling and increased seasonality (Cerling et al. 1998, Osborne 2007). Mammalian faunas from all continents experienced evolutionary changes within lineages (particularly herbivores), replacement of browsers with grazers, and in many cases an increase in immigration events (Eurasia: Badgley et al. 2005, van Dam 2006, Fortelius et al. 2006, North America: Barnosky 2001, Barnosky & Carrasco 2002, Janis et al. 2004, Hopkins 2007, Africa: Bobe 2006, South America:

Flynn et al. 2003, Pascual 2006, Australia: Long et al. 2003). The global generality of mid-Miocene changes indicates significant climatic impacts on mammalian faunas.

We highlight one particularly good stratigraphic sequence (the Siwalik sequence of Pakistan) that integrates evidence from a variety of sources (reviewed in Badgley et al. 2005). Turnover in the Siwaliks was found to be due both to tectonic forcing of climate and changing landscape and vegetation, particularly the dramatic change from C3-dominated closed forests to C3-open woodlands to C4-dominated open grasslands that occurred from 10.7 to 5.7 mya (Badgley et al. 2005). Analysis of this sequence shows that mammals predictably responded to climatic change, but they did so in a variety of ways. Species that were rare were less likely to survive through the climatic transition, whereas abundant species were more likely to persist. The mammalian response is concordant with predictions based on general traits such as whether they were dietary specialists or not. For example, the frugivores and browsers tied to forest vegetation disappeared during the transition to grassland and were replaced by grazing species (Badgley et al. 2008).

Plio-Pleistocene turnover events. The Plio-Pleistocene appears to be an important period of mammalian faunal change throughout the globe, for humans and other mammals. The onset of major cooling and drying ∼2.8 mya, which also corresponded to a shift in the periodicity of climate cycles and the onset of bipolar glaciation, drove a major turnover pulse in African bovids (Vrba 1995), micromammals (Wesselman 1995), and hominids (Vrba 1995). Bobe & Behrensmeyer (2004) confirmed that climate is associated with community change in African mammals, but linked hominid evolution to complex shifts in the environment of Africa between 2.8 and 1.8 mya instead of ascribing it to a continuous trend. Questions remain about the temporal distinctness and the climatic context since the data are not well compared to other Cenozoic baselines in Africa, but overall the shifting biota is coincident with changing climatic conditions

The Plio-Pleistocene saw community changes in other areas as well. For example, Raia et al. (2005) found that turnover rates were associated with shifts to cooler climate in large mammals from the Italian peninsula. At the same time, evolution in a rodent specialist occurred, whereas generalists exhibited stasis (Renaud et al. 2005). Additionally, new elephant taxa appeared on the Italian Peninsula during the Plio-Pleistocene due to immigration from Eastern Europe/Asia during climatic phases of lowered humidity (Palombo & Ferretti 2005). These data signify how particular, but potentially isolated geographic regions may exhibit unique temporal trends of community change and point to the need to integrate across regions during periods of global change.

A final significant change to global mammalian communities occurred at the end of the Pleistocene on all continents except Africa (reviewed in Koch & Barnosky 2006). Although the late Pleistocene-Holocene extinction event did not entail replacement of most continental faunas, it did involve a significant decrease in species richness and the immigration of modern humans into all continents. A significant proportion of large mammals were lost due to the combined effects of climate and human hunting (Koch & Barnosky 2006), altering the body size structure of extant communities (Smith et al. 2004).

LESSONS FROM THE FOSSIL RECORD

Climate has had significant impacts on mammals at all scales of time and space (**Figure 3**), and several important insights emerge that have implications for the role of global climate on the future of mammals. Most importantly, because multitaxon responses are the sum of climatic influence on processes operating at the single species level (i.e., population abundance, morphological change, genetic change, and range shifts), the immediate effects of climate will be most obvious

for individual species (**Figure 2**). Fossil evidence for clear effects of climate is most strongly seen at the individual species level, and we are already seeing clear signs of individual species response in modern populations (Parmesan 2006).

Climate clearly played a role in influencing mammalian turnover in the past. While examples of biotic turnover were often place or lineage based, the strength of species associations with particular habitats in determining biotic response seems robust. Additionally, biotic turnover during the PETM and at the MMCO, for example, reveals that the cumulative effects of impacts across many species simultaneously will result in significantly altered mammalian ecosystems. The potential for present and future biotic turnover, with many species in many ecosystems responding simultaneously, is truly alarming (Parmesan 2006). Considering that generation of novel mammalian species proceeds over much longer time spans than does immediate climatic change, that habitats are quickly being fragmented, and that species invasions are ubiquitous (Dirzo & Raven 2003), present mammalian diversity as we know it is in peril. Although we presented mammalian responses as largely independent, in most cases multiple responses occur simultaneously—even within a species. It is thus important also to look beyond these isolated features of species or single-taxon responses to the cascade of effects on functioning ecosystems, which is little synthesized and about which little is understood. Only then will we have an integrated and informed perspective about the full potential dynamics of mammalian ecosystems well into the future.

SUMMARY POINTS

1. Mammals clearly demonstrate sensitivity to climatic change through within-species responses, which range from changes in genetic diversity to shifting geographic ranges over hundreds to thousands of years. Over thousands to millions of years climatic change has induced the alteration of mammalian lineages and communities. These impacts were mediated through climatic changes over a wide variety of rates and magnitudes and in different environments (**Figure 3**). In general, the rates we detect from the fossil record are much lower than those projected for the near future even after adjusting for the coarser measurement intervals of the fossil record (**Figure 4**; Barnosky et al. 2003, Visser 2008). This has serious implications for the future of mammalian populations, given the high rate of climatic warming occurring today.

2. Many of the effects of climate on mammals will be enhanced, modulated, or buffered by changes to habitat, likely through factors other than just temperature, such as precipitation or seasonality. Those species that can track their preferred habitat as climates change via habitat corridors are the least likely to show genetic or phenotypic change. In contrast, species that are trapped in increasingly suboptimal habitats are most likely to experience increased selection and subsequent genetic and morphological change, which will be of particular concern for already-threatened small populations.

3. Many lines of evidence are converging on the roles that differential life histories, including body size and environmental buffering behaviors such as hibernation (Liow et al. 2008), community composition and history (Jernvall & Fortelius 2004), specialization versus generalization (Renaud et al. 2005), range size and location (Bruzgul & Hadly 2007), and commonness versus rarity (McGill et al. 2005), have on macroevolution. These studies, and others, point to additional important factors such as ecological sorting that, combined with insights from the fossil record (Vrba & Gould 1986), should be incorporated into

development of diversity models intended for the future (Berteaux et al. 2006). In particular, life history and modes of life may provide a general framework for predicting genetic diversity, abundance, geographic ranges size, species duration, sensitivity to habitat change and thus, overall extinction risk. A general model for this integration has not yet emerged.

4. Somewhat counterintuitively, the fossil record also demonstrates remarkable community stability in the face of climatic change (see Community Stability sidebar). Thus, although individual species may become extinct, it is possible that with enough available species redundancy, the functional relationships within communities may remain constant. However, this resilience depends on accessibility of communities to dispersers from other similar environments (Hubbell 2001). Maintaining habitat connections, and perhaps even facilitating exchange in extreme cases, may be necessary to maintain community structure. By losing habitat connections and corridors we have the potential to eliminate the very processes that have served to maintain these communities through geologic time.

5. Species invasions are understood to be important drivers of change in modern ecosystems. Lessons about immigration events from the fossil record demonstrate that there are often unpredictable outcomes of influxes of new species. Although novel species may sometimes solely enhance species richness, new species may replace the resident species, and experience increased rates of diversification in the process. General models predicting the likelihood of species invasions using insights from the fossil record are lacking.

FUTURE ISSUES

1. Many of the effects of climate change on mammals will be modulated by changes in habitat, perhaps through adjustments in precipitation or seasonality. However, we do not have a clear understanding about the role of global warming on local and regional precipitation and temperature patterns (Solomon et al. 2007a), and thus, are limited in our ability to predict what types of habitat changes will occur to particular species. More detailed integrative studies and development of local climatic models useful for historic as well as future climates will assist immensely with this understanding.

2. Single-taxon responses are among the clearest signs of the impact of climate on mammals in both the fossil and modern records. However, it is important also to look beyond isolated or single-process responses to the suite of responses in functioning ecosystems. These cascading effects are poorly understood for modern ecosystems and are almost nonexistent for extinct communities. No general model exists for the links between all these modes of ecological and evolutionary responses of individual species to climatic change. Thus, integration of environmental change into a model of the connections between mechanisms is one particularly fruitful area of future research.

3. Integration of data across different temporal and spatial scales (Riddle et al. 2008) will provide us with a powerful tool kit for predicting mammalian responses to future climate. The independence of different types of data, good chronologies, and robust phylogenies will enable us to use a hypothesis-testing approach to characterize the scale of mammalian responses and the spectrum of processes acting simultaneously, and will yield to a better assessment of the probability of each type of response in the future.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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