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# The Role of Climatic Change in the Evolution of Mammals

ANTHONY D. BARNOSKY AND BRIAN P. KRAATZ

*The paleontological record of mammals offers many examples of evolutionary change, which are well documented at many levels of the biological hierarchy—at the level of species (and above), populations, morphology, and, in ideal cases, even genes. The evolutionary changes developed against a backdrop of climatic change that took place on different scales, from rapid shifts in climate state that took only a few decades, to those that occurred over a millennial scale, to regular glacial–interglacial transitions with cycles of roughly a hundred thousand years, to long-term warming or cooling trends over hundreds of thousands to millions of years. Are there certain scales of climatic change that accelerate evolution? And what will the current global warming event do to evolutionary rates? Here we use paleontology—the study of fossils—to illustrate the scientific method behind answering such complex questions, and to suggest that current rates of global warming are far too fast to influence evolution much and instead are likely to accelerate extinctions.*

*Keywords: paleontology, evolution, mammals, scientific method, climate*

**D**espite all the arguments over semantics, evolution is a fact. It is a fact in the sense of dictionary definitions—for example, “something having real, demonstrable existence...the quality of being real or actual” (Soukhanov et al. 1996). And it is a fact in the scientific sense—“an observation that has been repeatedly confirmed” (Kennedy et al. 1998).

This is a bold statement, but it follows directly from incontrovertible observations. We know what genes are and how traits are inherited, and that the variation we observe between individuals within populations and between species is underlain by genetic differences. We know how those genetic differences arise and how they are maintained: through mutation, recombination, random drift, and selection. We can (and do) induce within-species evolution in domestic animal breeding programs—think of dogs, cattle, and racehorses. And we have seen natural selection cause evolution in such examples as industrial melanism in moths (Cook 2003, Rudge 2005) and the reduction of size in snow lotus plants (Law and Salick 2005). On the microbial level, we recognize the reality of evolution by spending money on it: As Palumbi (2005) pointed out, consumers and taxpayers spend billions of dollars to combat the ever-escalating evolutionary arms race between antibiotics and the new bacterial genomes for which they select, and to try to prevent such potentially disastrous pandemics as avian flu.

Observations from the fossil record show us how those mechanisms we observe in such a short term play out over the long term—which is somewhat remarkable, given that the fossilization process requires such a complicated sequence of events that only a tiny fraction of all the life forms that have ever lived were preserved as fossils, and a yet tinier fraction of those have been discovered. Darwin (1859) recognized

the limits of the fossil record in this regard, and his contemporary Thomas Huxley recognized its power in the evolutionary debate when he wrote, “Primary and direct evidence in favour of evolution can be furnished only by palæontology. The geological record, so soon as it approaches completeness, must, when properly questioned, yield either an affirmative or a negative answer: if evolution has taken place, there will its mark be left; if it has not taken place, there will lie its refutation” (Huxley 1880).

Although the paleontological record is still far from complete—for the same reasons Darwin and Huxley recognized some 150 years ago—it now yields a resounding affirmative answer about evolution. Fossils demonstrate overwhelmingly that geologically older species are replaced by geologically younger descendent species (including the succession of species in our own human history). The younger species typically share certain traits with the older ones, but

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have also added some new ones. This replacement of “less derived” by “more derived” species is so powerful that it is possible to slot almost any fossiliferous rock into a slice of time simply by identifying the fossil species within it (Pojeta and Springer 2001); it is the basis for the geologic time periods that students memorize, and on which energy companies rely to find the oil and gas that, for the time being, make our economically high standard of living possible.

In some cases, major evolutionary transitions are recorded in more detail than one might expect from the poor fossil record. For example, the transition from fish to tetrapods is beautifully documented by the fossil evidence of *Tiktaalik*, a fish whose appendages are intermediate between fish fins and tetrapod limbs (Daeschler et al. 2006), and the transition from dinosaurs to birds is illustrated by *Archaeopteryx* and other feathered dinosaurs (Pojeta and Springer 2001). There is similar evidence in the exquisite transformation of jaw bones into the bones of the middle ear in the evolutionary sequence that leads to true mammals (Pojeta and Springer 2001); in the shift from land-dwelling, two-toed, hoofed mammals to whales (Gingerich et al. 2001, Pojeta and Springer 2001, Thewissen and Bajpai 2001, Thewissen et al. 2001); and even in the development of uniquely human features such as bipedality and the expanded human brain, as traced from *Homo erectus* to *Homo sapiens* (Kennedy et al. 1998, White 2002, White et al. 2006).

At its finest, the fossil record offers snapshots of one species evolving into the next, in the form of transitional morphologies that actually make it difficult to distinguish the boundaries between species. Such morphological transitions at the species level (and in some cases, even the population level) are all the more noteworthy because it is probable that most species arise through geologically fast-branching events (Eldredge and Gould 1972, Gould 2002). That, in combination with the vagaries of the fossil record, would seem to make it unlikely to find fossils that actually record the transition of one species into its descendant species—yet paleontology yields those examples in organisms as diverse as foraminifera (Malmgren and Kennett 1981, 1983), mollusks (Williamson 1981, 1985), voles (Barnosky 1987, Barnosky and Bell 2003), pocket mice (Carrasco 1998), hoofed herbivores (Gingerich 1985), horses (MacFadden 2005), mammoths (Barnosky 1987, Lister and Sher 2001, Lister et al. 2005), elephants (Barnosky 1987), and even species of the hominid genus *Australopithecus* (White et al. 2006).

Evolution is also a theory—but only in the sense that scientists define that word: “systematically organized knowledge applicable in a relatively wide variety of circumstances, especially a system of assumptions, accepted principles, and rules of procedure devised to analyze, predict, or otherwise explain the nature or behavior of a specified set of phenomena” (Soukhanov et al. 1996). It is not a theory in the sense that proponents of creationism or intelligent design use the word: “an assumption based on limited information or knowledge; a conjecture” (Soukhanov et al. 1996). Scientific theories are founded on the satisfactory answers to huge numbers

of past questions, and they also lead to new questions as we seek to refine our knowledge.

Where, then, are the unanswered questions about evolution, and how do we look for the answers? One of the more intriguing questions is whether pulses of speciation—the origin of new species from old ones—are driven by interactions between species in the absence of environmental changes (like climatic change), or whether environmental changes are actually required to cause some of the rapid evolutionary events observed in the fossil record. This question is all the more intriguing in view of current, human-caused global warming, which is changing the climate at a rate faster than Earth has experienced for at least 60 million years (Houghton et al. 2001, Barnosky et al. 2003). How do we forecast the evolutionary effects of such a fast rate of change? If climatic change at this pace does not cause speciation, the question is moot. If climatic change actually stimulates evolution, could we see new species originating, which could counteract biodiversity losses caused by other human impacts? And if climatic change at this pace is too fast for evolution to keep up, will biodiversity decrease as extinction outpaces evolutionary change? Here we use the fossil record of mammals to address these questions, and also to demonstrate the scientific method behind using paleontological data to study evolution and forecast future events.

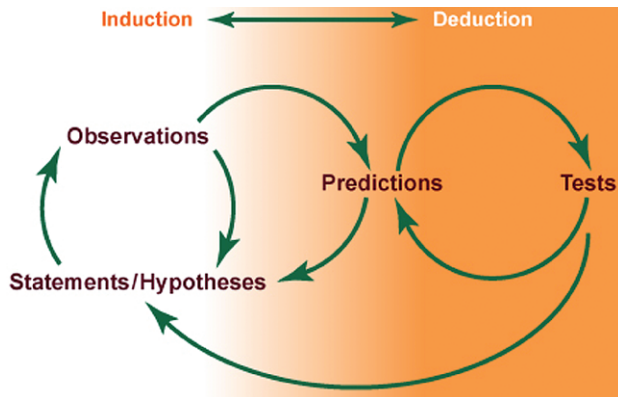
### The scientific method and paleontology

Science proceeds by using observations to formulate hypotheses, then testing the predictions of the hypotheses through controlled or natural experiments to see if the predictions hold true (figure 1). Controlled experiments are set up by an investigator such that certain parameters can be held constant and others can be varied. Natural experiments are those that nature has already run, leaving data that scientists can use.

In contrast to the linear progression often presented in textbooks, the process of doing science actually is iterative (figure 1). The scientific method is actually a scientific loop, with fluid transitions between inductive reasoning (in which general principles are extrapolated from specific observations) and deductive reasoning (in which a generally accepted principle is used to explain a specific observation). This scientific loop characterizes all science, no matter whether experiments are controlled or natural.

In paleontology, the observations are based on fossils and their living relatives. Usually, natural experiments are the modus operandi, although in certain cases controlled experiments are possible. Predictions involve projecting what one would expect to find in deep time if processes observable over human lifetimes accumulated, or what would be expected in a new fossil locality on the basis of what had already been found in previous localities. Tests are provided by the fossils themselves, which are the primary data, and by their enclosing sediments.

In the ensuing discussion, we apply this basic scientific methodology to our specific questions about evolution and



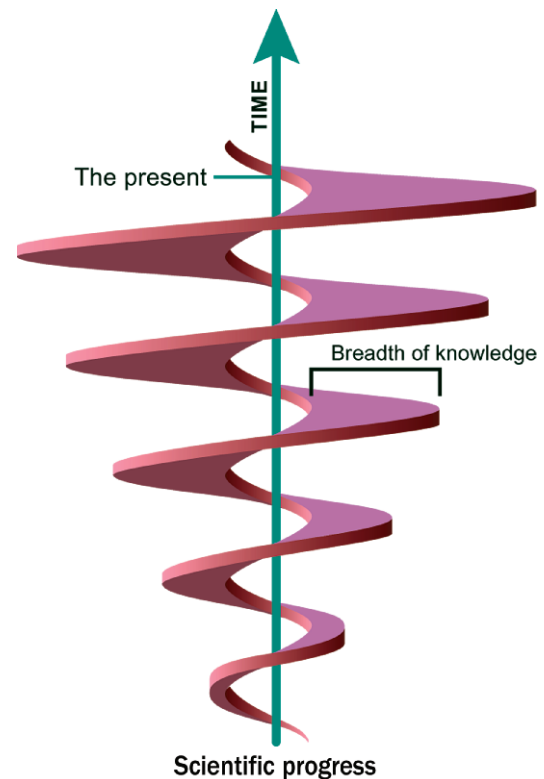
**Figure 1.** Diagram showing the major components of the scientific method, more appropriately regarded as a scientific loop. Observations are what we observe in the natural world through our senses. Hypotheses are general statements to explain observations, for example, that the observations result from a certain mechanism. Predictions are what we would expect to see if the hypothesis is correct. Tests require generating or finding data to see if a given prediction holds true. If the data match the prediction, the hypothesis gains strength, but if the data differ from what was predicted, the hypothesis is rejected or modified. Arrows show the iterative nature of science: Testing predictions leads to new observations, which lead to modifying old hypotheses or formulating new hypotheses, which in turn leads to new predictions and tests. Figure by Brian P. Kraatz and David K. Smith.

climatic change. However, it is important to note that through the same kind of iterative observation, prediction, and tests, evolution itself has proceeded from hypothesis in Charles Darwin's time to scientific fact in ours, following the trajectory schematically illustrated in figure 2.

### Observations

Although one can be drawn into the scientific process at any point in the cycle illustrated in figure 1, in practice the starting point is often with observations. In using paleontology to understand how climatic change affects evolution, we start with five related observations: (1) Evolution can be recognized at different scales of the biological hierarchy, from molecules to relationships among species. (2) Climate is known to change on various timescales and geographic scales. (3) Climatic changes observed over a few decades are known to correlate with changes in living populations and species. (4) There are some theoretical reasons to expect the kinds of apparently climate-driven changes in populations and species that we observe today to play out as accelerated speciation over the course of thousands or millions of years. (5) The fossil record shows many changes in geographic range and many speciation events in mammals over the last 65 million years.

**Scales of evolutionary change.** In paleontology, the details of evolution can be studied most easily at two levels of the



**Figure 2.** Diagram showing how the scientific process leads to progressive understanding. Over time, as predictions are repeatedly confirmed through multiple tests, hypotheses are transformed into scientific fact, and the foundation of scientific knowledge becomes more and more robust. In the context of evolution, Charles Darwin's *Origin of Species* would fall near the bottom of this diagram, and the ever-widening upward spiral would be the body of knowledge that has grown from iterative development of hypotheses, predictions, and tests confirming that evolution takes place. Figure by Brian P. Kraatz and David K. Smith.

biological hierarchy: populations and species. Populations are groups of individuals that regularly share genes—that is, groups of interbreeding animals that live relatively close together. Species are usually made up of many populations.

When we talk about evolution at the population level, ultimately we are talking about changes in gene frequencies across generations. Sometimes animals from one population disperse and find a mate in another population, resulting in gene flow between populations. If gene flow is sufficiently reduced, two populations can diverge genetically and have the potential to become different species, but such populations still have the potential to intermingle and lose their genetic distinctiveness, should the right conditions bring them back into contact (Barnosky 2005 and references therein).

When we talk about a speciation event, we mean that a population has changed its genetic composition to the extent

that its individuals can no longer mate with those from different populations and produce viable offspring under natural conditions. It is therefore a new species, because it has attained its own evolutionary trajectory, distinct from that of the parent population or other populations. This biological species concept seems to serve well for mammals and for our purposes, although other species concepts exist (see the review and additional references in Barnosky 2005).

In exceptional cases, we can recognize population-level evolution and speciation in the fossil record by observing changes at the genetic level. However, usually the morphology of teeth, skulls, and other bones is used as a proxy for genetic differences, because genetic material is not commonly preserved in fossils older than a few thousand years. Studies have confirmed the general validity of using differences in phenotype to infer differences in genotype in many cases (Jernvall and Jung 2000, Salazar-Ciudad and Jernvall 2002, Polly 2003a, 2003b, Salazar-Ciudad et al. 2003), though much remains to be learned about the details of how genotype relates to phenotype.

**Scales of climatic change.** In essence, climate is the average weather over many years. But how many years? That question is at the root of what we mean by scales of climatic change. A number of studies have used paleontological and geological data to trace how climate has changed at a variety of scales through Earth's history. Among the most important paleoclimate proxy data (serving to some extent as "paleothermometers") are oxygen-isotope ratios from fossil foraminifera, vegetation records from fossil pollen, and samples of the ancient atmosphere trapped within bubbles in glacier ice (Ruddiman 2001). Observations from these sources of data typically begin by coring the ocean bottom, lake sediments, or ice; sampling the core at regular intervals (the oldest samples are at the bottom, the youngest at the top of the core); and using a variety of techniques to analyze each sample in order to infer some aspect of what the climate was like when the organisms were alive (or, in the case of ice cores, when the atmospheric gas was trapped in the ice). Such data sources have led to robust reconstructions of past climate, because the patterns they show independently are congruent with one another (Bradley 1999, Ruddiman 2001).

Such information, augmented by many other kinds of paleoclimate proxy data (Birks and Birks 1980, Bradley 1999, Ruddiman 2001), reveals four timescales of climatic change that might reasonably be expected to match the rate at which evolutionary changes would be expected to be evident: the tectonic, orbital, deglacial millennial, and historical (figure 3; Ruddiman 2001). The tectonic timescale, so named because it is measured over the same extremely long time periods (millions of years) it takes for tectonic activities to build mountains, is characterized by an overall warming of Earth between about 300 million and 100 million years ago, followed by cooling (figure 3a). In the last 65 million years of the tectonic scale (the time mammals were abundant on Earth), superimposed on the general cooling was a warming event called the Mid-

Miocene Climatic Optimum, which lasted from about 18.5 million to 14 million years ago (figure 4). In the first 1.5 million years of this climatic event, the mean global temperature rose 3 degrees Celsius ( $^{\circ}\text{C}$ ) to  $4^{\circ}\text{C}$ , and these warm conditions persisted for the ensuing 3.5 million years (Zachos et al. 2001, Barnosky et al. 2003).

Zooming in on just the last 3 million years of the tectonic timescale reveals the orbital scale, with the last 1.8 million years, in particular, being characterized by the cyclical flip-flop of glacial and interglacial cycles (figure 3b). At this temporal scale, measured in hundreds of thousands of years, each cold-warm cycle lasted about 41,000 years until about 1 million years ago, when the cycles increased in amplitude (greater difference between warmer and colder extremes) and began to take about 100,000 years per cycle. In the 100,000-year cycles, the cold glacial spells last for most of the cycle; changes from a glacial to an interglacial period involve warming global temperature about  $5^{\circ}\text{C}$  within 5000 years (though much of the total change probably occurs in a much shorter period); and the interglacial periods (such as the one we are in now) last about 10,000 to 20,000 years (Raymo 1992, 1997, Raymo et al. 1997, Schmieder et al. 2000, Barnosky et al. 2003).

The deglacial millennial scale (figure 3c), measured in thousands of years, focuses on the last cold-warm transition, beginning about 50,000 years ago. At that finer resolution, each glacial or interglacial stage has many climatic oscillations embedded within it, some of which take place over decades to centuries and cause mean global temperature oscillations that, although short-lived, can be up to  $9^{\circ}\text{C}$  within 50 years (Raymo et al. 1998, Severinghaus and Brook 1999, Blunier and Brook 2001, Barnosky et al. 2003).

At the historic timescale, measured in hundreds to tens of years, even shorter-term but lower-amplitude oscillations are apparent, as exemplified by the last 3000 years of the present interglacial stage (figure 3d). Of particular note is the Medieval Warm Period, which lasted from about 750 to 1150 years ago and was characterized by warming of about  $1^{\circ}\text{C}$  within its first 100 years (Hughes and Diaz 1994, Campbell et al. 1998, Broecker 2001, Barnosky et al. 2003).

Finally, scientists can use computer models that integrate historic data to project how climate will change in the next hundred years under varying scenarios of increasing concentrations of carbon dioxide. Those changes are measured over tens of years. Even when temporal scaling factors are adjusted for, the predicted warming of  $1.4^{\circ}\text{C}$  to  $5.8^{\circ}\text{C}$  for the years 1990 to 2100 is at a much faster rate than has been typical throughout mammalian evolution (Houghton et al. 2001, Reilly et al. 2001, Wigley and Raper 2001, Barnosky et al. 2003). The faster than normal rate is upheld by the most recent studies, which indicate that warming will be somewhere between  $1.1^{\circ}\text{C}$  and  $6.4^{\circ}\text{C}$ , most likely between  $1.8^{\circ}\text{C}$  and  $4.0^{\circ}\text{C}$  (Alley et al. 2007).

Climate varies spatially as well as temporally (Houghton et al. 2001, Ruddiman 2001): For example, even though we can specify a mean global temperature for Earth as a whole, the mean temperature of Alaska is much different from the



mean temperature of Florida. Therefore, in assessing the role of climatic change in evolution, it is important to match the fossil data geographically with the climate data. Lumping too many geographic regions potentially masks real responses, because opposite responses in different regions tend to hold an average constant (Barnosky 2001, Houghton et al. 2001, Ruddiman 2001, Barnosky and Carrasco 2002).

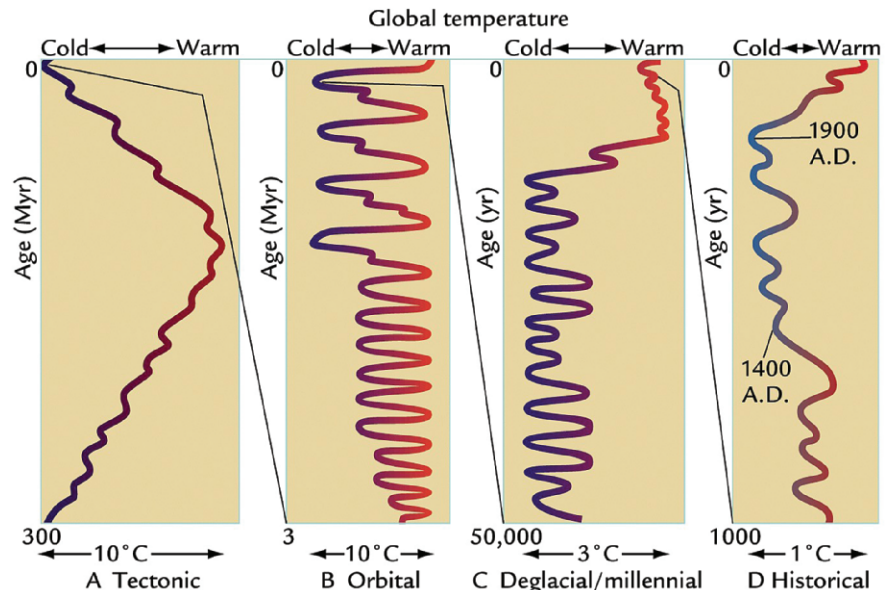
### Response to observed climatic change.

Several studies have shown correlations between climate trends over the past 50 years or so and changes in the geographic range of species, in population density, or in other parameters that influence how many offspring are produced. Such effects have been observed in diverse mammals, such as deer, moose, caribou, musk oxen, bighorn sheep, African antelope, foxes, marmots, and pikas (Inouye et al. 2000, Niemelä et al. 2001, Patterson and Power 2002, Post and Forchhammer 2002, Walther et al. 2002, Ogutu and Owen-Smith 2003, Root et al. 2003, Grayson 2005). Thus, it seems likely that climatic changes influence how animals are distributed on the landscape and the likelihood that they will persist in a given place.

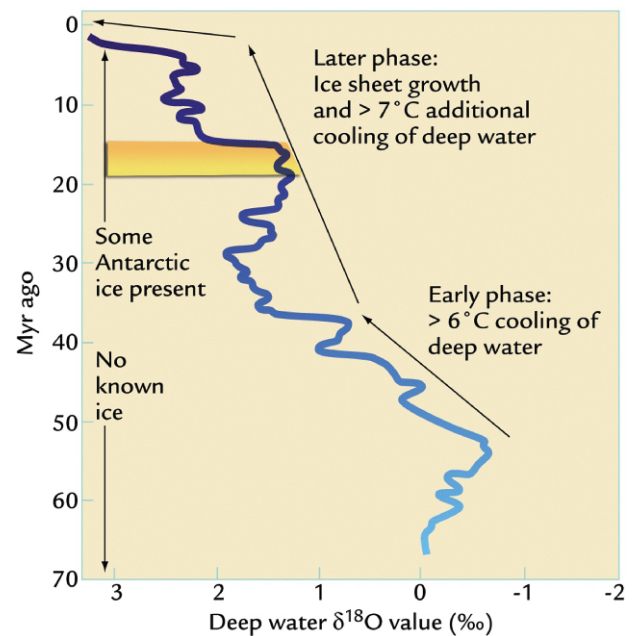
**Potential links between climate-driven range changes and speciation.** The fossil record documents that speciation takes place, and there are several different models of how the details work (Coyne and Orr 1998, Gavrilets et al. 1998, Mallet 2001, Schluter 2001, Via 2001, Wu 2001). Under most models, chances for speciation increase when small, isolated populations are subjected to new, strong selection pressures (Vrba 1995, Barton 2001, Rosenzweig 2001, Vrba and DeGusta 2004). Therefore, the kinds of changes in mammal species ranges and population densities that have been shown to correlate with climatic change are logical candidates for leading to speciation, because changes in climate can (a) fragment species ranges as climate zones shift across the earth's surface, (b) cause populations to disperse and become isolated as they track their preferred climate, and (c) result in new selection pressures when populations inhabit new climates (Barnosky 2005).

### Past changes in geographic ranges and speciation events.

Links between climatic change and species distributions are suggested by the changes in species ranges from the last part of the Pleistocene (the last time Earth was in a glacial stage) through the early part of the Holocene (when the present interglacial stage began) and historic times. In most cases for which the fossil record is good, dramatic range shifts are evi-



**Figure 3.** Different scales of climatic change. Time is on the vertical axis. The oscillating lines symbolize the periodicity and amplitude of temperature changes that Earth experiences on different timescales. The overall pattern is one of successively more rapid oscillations of climate being nested within less rapid oscillations. Figure reprinted from Ruddiman (2001). © 2001 by W. H. Freeman and Company. Used with permission.



**Figure 4.** Detail of the last 70 million years of climatic change at the tectonic scale. The shaded interval is the Mid-Miocene Climatic Optimum. Figure modified from Ruddiman (2001). © 2001 by W. H. Freeman and Company. Used with permission.

dent (FAUNMAP Working Group 1996). Looking back millions of years, changes in species ranges also are evident as species go through time (Carrasco et al. 2005), and it is pos-

sible to divide the last 65 million years into at least 39 distinct intervals defined solely by the species of mammals that characterized each interval (the so-called North American Land Mammal Ages and subdivisions thereof; Woodburne 2004). Therefore, it is clear that species wax and wane through geographic space as well as through time, that new species have arisen through speciation events and older species have gone extinct, and that all of this has taken place against a backdrop of climatic change of varying scales.

### From observations to hypotheses

These observations lead to many possible explanations for how climatic change might interact with evolution. Most involve determining whether or not range changes, speciation, and extinction events corresponded in time with, and therefore potentially were caused by, climatic changes. That determination requires asking pertinent questions that can be formulated into testable hypotheses. Here we settle on four questions that can be addressed with natural experiments that have already been analyzed (table 1). Many other questions and hypotheses could be generated, some of which, like our examples, could be addressed using data that already exist, and others of which would require fieldwork and additional analyses to gather the relevant data. Whatever the question, the scientific loop (figure 1) transforms observations into questions, and each question into a hypothesis (table 1).

### Testing predictions

Hypotheses are a way of framing questions such that they yield specific predictions. Those predictions can then be tested with data; if the data are at odds with the prediction, the hypothesis loses credibility or is rejected outright. Often, testing predictions yields new observations that go back into the scientific loop and end up in modified hypotheses. Table 1 lists the predictions for each of our hypotheses.

**Effects of historical climatic change.** Data to test the predictions of our first hypothesis (“Changes in climate cause genetic changes in populations”; table 1) come from Yellowstone National Park, where paleontologists and biologists (Hadly

1996, 1999) have compared mitochondrial DNA (mDNA) from fossil populations that track the last 3000 years with mDNA from modern populations through a wide part of the geographic range of the analyzed species. The two species that were studied are the northern pocket gopher (*Thomomys talpoides*) and the montane vole (*Microtus montanus*) (Hadly et al. 1998, 2004). Each pocket gopher typically spends most of its life in its burrow, and individuals do not stray far from where they were born; thus, populations tend to have little spatial gene flow. In contrast, montane voles spend most of their life on the surface, scurrying along “vole runways” through grass or under the snow, and individuals commonly disperse away from where they were born. Both species prefer relatively moist microhabitats, and Hadly and colleagues (1998, 2004) found that, as expected, when the climate in Yellowstone warmed during the Medieval Warm Period, population sizes in each species declined.

However, the genetic effects of that climate-driven population decline were very different in the two species. For the gophers, the onset of the Medieval Warm Period saw a decline in genetic diversity, as climate caused populations to decrease in size. This fits the predictions of population biology theory: As fewer individuals remain in the gene pool, genetic variation decreases. In voles, however, the reduction in population size went along with an increase in genetic diversity. This is because, even though densities of the vole populations endemic to the study site in Yellowstone decreased, dispersers from other populations continued to flow in from elsewhere, bringing with them their distinctive genotypes.

These data support the hypothesis that climatic change effects genetic change, because they accord with the predictions of that hypothesis. But they also lead to two new observations that must now be incorporated: (1) Species with different life history strategies are affected differently, and (2) the genetic change observed during the Medieval Warm Period, while significant at the population level, did not lead to speciation. With these observations, we can reject any hypotheses predicting that climatic change similar in magnitude to that of the Medieval Warm Period will cause speciation in these kinds of species, and also reject any hypotheses that

**Table 1. Iterative process from questions to hypotheses and testable predictions.**

| Question  | Hypothesis   | Prediction   |
|---|--|--|
| 1. Does climatic change stimulate changes at the genetic level?                                       | Changes in climate cause genetic changes in populations.   | Populations traced through the Medieval Warm Period will show genetic changes that coincide with climatic changes.   |
| 2. If so, do those changes accumulate to cause speciation at the orbital climate scale?               | Speciation is accelerated by the cyclical climatic changes that occur at the orbital scale.  | Clusters of speciation events should be evident within the last two million years (the ice ages).  |
| 3. Or does the pace of climatic changes have to be at the tectonic timescale to stimulate speciation? | Speciation requires out-of-the-ordinary climatic changes that take place at the tectonic scale; shorter periods of climatic change do not give evolution enough time to operate. | Clusters of speciation events should occur at the same time as climatic changes such as the Mid-Miocene Climatic Optimum, but not when climatic events occurred at shorter timescales. |
| 4. Will global warming over the next century accelerate speciation?                                   | The current rate of global warming is so fast that evolution cannot keep up.   | Extinction rates will outpace evolution, and many species will go extinct.   |

would require a uniform genetic response in all species. But the observations are entirely consistent with climate having some influence on the speciation process, so it becomes worthwhile to progress to the second question in table 1: If there are more severe climatic changes that last longer than the Medieval Warm Period, might the kinds of genetic effects we observe lead to speciation?

**Effects of orbital and deglacial millennial climatic change.** Two kinds of tests can be conducted to determine whether speciation events cluster at glacial–interglacial transitions evident on orbital and deglacial millennial climate scales. First, as we did for the Medieval Warm Period, we can trace populations through the pertinent time spans—in this case hundreds of thousands of years. Such data are hard to come by, but one place where this is possible is in the high Rocky Mountains of Colorado, at a site called Porcupine Cave (Barnosky and Bell 2003, Barnosky 2004, Barnosky et al. 2004). The deposits within Porcupine Cave contain thousands of mammal fossils distributed through sediments that accumulated from approximately 1 million to 750 thousand years ago. By tracing the changes in details of the teeth of certain mammals through that 250,000 years, it is possible to observe in a general way whether the gene pool was influenced by the two glacial–interglacial transitions that are represented in the deposit, both of them older than 750,000 years.

As was the case with the Medieval Warm Period, two species with differing life history strategies were examined. Marmots (*Marmota* sp.) showed no detectible response to glacial–interglacial cycles, possibly because they hibernate in burrows, where effective microclimates remain fairly stable, during fall, winter, and spring. In contrast, the sagebrush vole (*Lemmiscus curtatus*), which lives aboveground throughout the year, demonstrated dental changes at one (but not the other) glacial–interglacial transition. That transition was the one that corresponded to the most pronounced climatic change in the sequence. The changes that took place were slight differences in tooth shape that affect how well the teeth stand up to wear (see the illustrations in Barnosky and Bell 2003). The morphologic changes suggested genetic differences between the populations that lived during a particularly moist glacial period, when relatively soft vegetation was abundant, compared with those that lived during an exceptionally dry interglacial period, when on the whole the vegetation the animals ate was more abrasive to teeth. As in the Medieval Warm Period test, there is no evidence that a new species appeared coincident with the climatic change; instead, there was evolution within species.

This evidence is contrary to the prediction that speciation should cluster at glacial–interglacial transitions. However, before that hypothesis can be firmly rejected, we need to make sure the marmots and sagebrush voles are not just exceptions to the rule.

The second kind of test again uses data from mtDNA, but this time exclusively from living mammals. By looking at the genetic difference between closely related populations within

the same species, it is possible to estimate how far back in time those two populations shared a common ancestor, that is, how long ago they branched off from a common parent population. Likewise, we can look at the difference between closely related species to see how far back in time the sister species shared a common ancestor. This kind of analysis has been performed for many different populations and species (Avice et al. 1998). If the orbital to deglacial millennial climate scales drive speciation, we would predict that a higher than average number of species should have diverged during the last 1.8 million years (when the ice ages were in full swing), or, if some glacial–interglacial transitions were more important than others, many species should have diverged at those particular climatic transitions.

The data do not fit this prediction (Barnosky 2005). When the calculated times of divergence are plotted against geologic time, the numbers of extant species that originated during the ice ages are no higher than one would expect, given the background rate of speciation events over the past 65 million years. However, nearly three-quarters of extant populations trace their ancestry back to the ice ages. These findings suggest that although the glacial–interglacial cycles stimulate evolution at the population level, those populations do not stay isolated long enough to turn into new species. Therefore, the evidence for climate influencing genetic change within populations gains more support with these tests, but the hypothesis that the orbital and deglacial millennial climate scales drive speciation can be rejected.

Is this because the climatic change at this scale is still too minor, or because of the cycling effect—that is, even though isolation and genetic change within a population may take place in one cycle, the next cycle erases any genetic changes that may have eventually led to speciation? To begin to answer that, we move on to the third question in table 1: Does the pace of climatic changes have to be at the tectonic timescale to stimulate speciation?

**Effects of tectonic-scale climatic change.** To test the idea that climatic changes that take place over the tectonic scale influence speciation, we rely primarily on the morphology of fossils to construct a family tree of species. The technique is phylogenetic analysis—a reasonably objective way to decide which species are most closely related to each other, and which are older or more recent. Each morphological trait of a fossil is evaluated; a matrix is constructed to indicate which fossils have which traits; and computer algorithms use the matrix to sort out a family tree on the basis of which species share newly appearing (derived) traits and which derived traits are unique to each species. Fossils are dated by various geological techniques, such as argon–argon or magnetostratigraphic dating (Pojeta and Springer 2001); thus, the branch points on the tree can be temporally bracketed within certain limits. Many branching events clustered together should reflect multiple speciation events within geologically short time intervals. If those clusters of branching events line up in time with the climatic changes of interest, the hy-



pothesis that the climatic change helped drive speciation cannot be rejected; on the other hand, random distribution of the branching points relative to the climate event would be grounds for rejection.

As with the tests for other scales of climatic change, we use information from two very different kinds of mammals: rodents of the mountain beaver family (apodontoids) and horses. Both groups have been well studied, and the fossil record of both is reasonably rich for the time periods of interest (Hopkins 2005, MacFadden 2005). Despite their name, mountain beavers are digging rodents (figure 5), not true beavers; they are even in a different family than true beavers. They include more than 30 species that lived during the past 35 million years, but only one surviving species today (*Aplodontia rufa*, in the Pacific Northwest).

More than 20 of the 30-plus mountain beaver species first appeared near the beginning of the Mid-Miocene Climatic Optimum (Hopkins 2005). Likewise, a burst of new horse species appeared at about the same time (MacFadden 2005). Such data agree with the expectations of climatic change stimulating speciation at this geographic (western United States) and tectonic scale (3°C to 4°C over 1.5 million years, followed by 3.5 million years of sustained warmth). Therefore, with this evidence, there is no reason to reject the hypothesis that speciation requires out-of-the-ordinary climatic changes at the tectonic scale (hypothesis 3 in table 1). However, before this hypothesis reaches the status of general acceptance, it would be desirable to have additional tests provided by robustly constructed and calibrated phylogenies of other mammal groups.

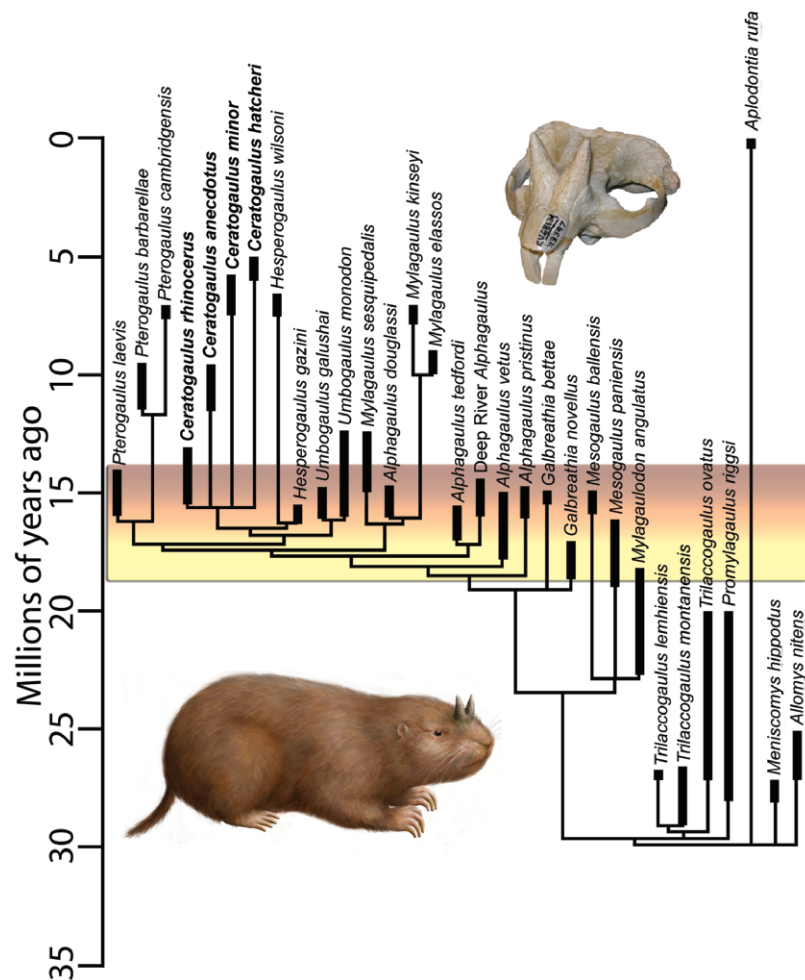
### Global warming over the next century

Testing the previous hypotheses yielded three new observations, which in turn lead, through hypotheses, to informed predictions about what to expect in the face of current global warming. In effect, we use what we have learned from the fossil record to make predictions about the future.

The tests discussed above yielded the following observations: (a) The different temporal and geographic scales of climatic change manifest at different evolutionary scales—some at genetic or population levels, others at the species level; (b) geologically rapid or cyclical climatic changes—from historic to orbital scales—cause genetic changes at the population level, but do not by themselves cause speciation (in part because isolation does not persist long enough at these scales); and (c) available evidence suggests that, to turn population-level evolution into speciation, climatic change must be unusual at the tectonic scale. The only test that indi-

cated speciation could occur on shorter timescales featured a climatic change that was unusual in respect to the climate of the previous several hundred thousand years, and was followed by the persistence of the new climatic regime for a very long time (hundreds of thousands to a million or so years).

Applying those observations to what we might expect in the future, it seems likely that we will see changes in genotypes and phenotypes at the population level in response to climatic change over the next hundred years. But climate-induced speciation, if it is a real phenomenon, appears to require climatic events that operate on a much longer timescale than those that can cause population-level response. So we would not expect speciation to regenerate biodiversity in response to human-induced global warming—especially keeping in mind that the rate of climatic change over the next century is likely to be faster than the rates experienced by mammals through much (if not all) of their evolutionary history.



**Figure 5. Phylogeny of mountain beavers (apodontoid rodents), which suggests that most speciation in this group was associated with the Mid-Miocene Climatic Optimum (shaded interval). One representative of this group (*Ceratogaulus*, in boldface) was a rodent with horns (see skull, upper right, and artist's rendition, lower left). Most of these species show some adaptations to a burrowing lifestyle. Phylogeny courtesy of Hopkins (2005); rodent reconstruction by Cheng (Lily) Li; skull photograph by David K. Smith.**

There may be an evolutionary danger in such fast rates of climatic change: Will selective pressures induced by climate be changing so fast that evolutionary adaptations simply cannot keep up? The fate for populations that experience such an effect is extinction; when too many populations decline in size and number, extinction follows for the entire species. One way for species to avoid that fate is to follow climate zones as they move around Earth's surface during times of changing climate—that is, to adjust their biogeographic range. Although many mammal species have done just that when climate changed in the past (FAUNMAP Working Group 1996, Carrasco et al. 2005), that option is less available today than before, because there is such a heavy human footprint on the landscape. Cities, highways, dams, farms, ranches—all of these and more are barriers to the natural movements of wild species.

These considerations lead to the final hypothesis in table 1—that rates of evolution, even at the population level, will be outpaced by human-induced climatic change. The prediction is a dire one: Extinctions may so far outweigh evolutionary additions to biodiversity that our grandchildren will live in a much-diminished world. The natural experiment needed to test that prediction is running right now. It is still unclear whether humanity will (or can) influence its outcome.

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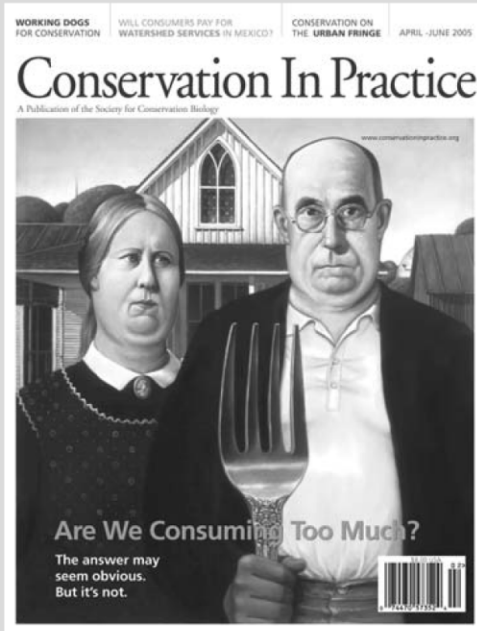
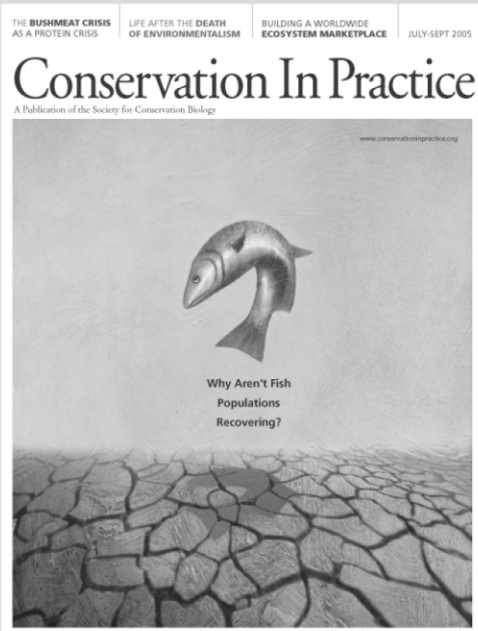
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