

Effects of Quaternary Climatic Change on Speciation in Mammals

Anthony D. Barnosky^{1,2}

An ongoing controversy in evolutionary biology is the extent to which climatic changes drive evolutionary processes. On the one hand are “Red Queen” hypotheses, which maintain that climatic change is less important than biotic interactions in causing evolutionary change. On the other hand are “Court Jester” models, which recognize climatic change as a very important stimulus to speciation. The Quaternary Period (the last 1.8 million years), characterized by multiple climatic changes in the form of glacial–interglacial transitions, offers a fertile testing ground for ascertaining whether cyclical climatic changes that operate at the 100,000-year time scale appreciably influence evolutionary patterns in mammals. Despite the increased potential for isolation of populations that should occur with multiple advances and retreats of glaciers and rearrangement of climatic zones, empirical data suggests that speciation rates were neither appreciably elevated for Quaternary mammals, nor strongly correlated with glacial–interglacial transitions. Abundant evidence attests to population-level changes within the Quaternary, but these did not usually lead to the origin of new species. This suggests that if climatic change does influence speciation rates in mammals, it does so over time scales longer than a typical glacial–interglacial cycle.

KEY WORDS: quaternary, mammals, speciation, climatic change.

INTRODUCTION

Although different models of have been proposed to explain how new species arise (Coyne and Orr, 1998; Gavrillets *et al.*, 1998; Mallet, 2001; Schluter, 2001; Via, 2001; Wu, 2001), many workers agree that the chances for speciation increase when vicariant or dispersal events result in small, isolated populations that are subjected to new, strong selection pressures (Vrba, 1995b; Barton, 2001; Rosenzweig, 2001; Vrba and DeGusta, 2004). Therefore, climatic change potentially provides a potent mechanism to force speciation, because it (a) introduces vicariant barriers as climate zones shift across the Earth’s surface; (b) can encourage dispersal as populations track preferred climate space; (c) can force isolation of small populations by either (a) or (b); and (d) can result in new selection pressures when populations inhabit new climate space. For these reasons, climatic change

¹Department of Integrative Biology and Museums of Paleontology and Vertebrate Zoology, University of California, Berkeley, CA 94720, USA.

²To whom correspondence should be addressed at Department of Integrative Biology and Museums of Paleontology and Vertebrate Zoology, University of California, Berkeley, CA 94720, USA. E-mail: barnosky@berkeley.edu

has been posited as a major driver of evolution (Janis, 1989, 1993, 1997; Janis and Wilhelm, 1993; Vrba, 1993, 1995a,b; Janis *et al.*, 2000; Vrba and DeGusta, 2004). The alternative view is that climatic change is “background noise,” to which species must be adapted if they are going to survive over long time spans, and that the major motor of evolutionary change is interactions between organisms (Van Valen, 1973; Alroy, 1996, 1998; Prothero and Heaton, 1996; Bennett, 1997; Prothero, 1999; Alroy *et al.*, 2000). Models that highlight the potential importance of climatic change include the Stationary Model (Stenseth and Maynard, 1984), Turnover-Pulse Model (Vrba, 1993, 1995b), Habitat Theory (Vrba, 1992), Traffic Light Model (Vrba, 1995b), Relay Model (Vrba, 1995b), and to some extent Coordinated Stasis (Brett and Baird, 1995) and Co-evolutionary Disequilibrium (Graham and Lundelius, 1984); elsewhere I have grouped these as Court Jester models (Barnosky, 2001), and noted that those that regard climatic change as background noise include various interpretations of Red Queen hypotheses (Van Valen, 1973).

One of the most dramatic times of climatic change in Earth history is the Quaternary Period, which encompasses approximately the last 1.8 million years. Composed of the Pleistocene and the current Holocene Epochs, the Quaternary was characterized by as many as 20 glacial advances and retreats. These dramatic climatic oscillations provide an ideal natural experiment with which to assess climate’s role in evolution. In the northern hemisphere, ice encroached into temperate latitudes of North America and Eurasia; in the southern hemisphere, mountain glaciers grew to vast proportions. With each advance and retreat of ice, coastal areas were alternately exposed and submerged, opening and closing dispersal corridors on a continental scale, for example, between Eurasia and North America. Accompanying these physical changes on the landscape were climatic changes in obvious parameters such as changes in mean annual temperature or precipitation in given areas, and also more subtle changes such as dramatic changes in seasonality, in atmospheric and oceanic circulation patterns, in monsoonal activity, in storm tracks, and in vegetational assemblages (Ruddiman *et al.*, 1989; Dansgaard *et al.*, 1993; Raymo, 1997, 1998; Raymo *et al.*, 1997, 1998; Kutzbach *et al.*, 1998; Clark *et al.*, 1999; Petit *et al.*, 1999; Schmieder *et al.*, 2000; Ruddiman, 2001).

Moreover, these changes were relatively rapid by geological standards (though slow in ecological time). For the first half of the Quaternary, each glacial–interglacial cycle lasted about 41,000 years, but beginning about 1,000,000 years ago, the cycles began to last about 100,000 years (Raymo *et al.*, 1997, 1998; Raymo, 1998; Schmieder *et al.*, 2000). The transition between glacial and interglacials was relatively quick—each 100,000 year cycle was characterized by ~10,000 years of maximum glaciation, followed by a transition that lasted less than a few millennia, into ~10,000 years of maximum interglacial warmth. Maximum warmth was then followed by 80,000 years over which conditions declined back to full glacial conditions (Ruddiman, 2001).

Transitions between glacial and interglacial climate states were further characterized by very rapid, high-amplitude climatic oscillations that took place within a few hundred years, for example, the Younger Dryas event that marked the most recent glacial–interglacial transition about 11,000 radiocarbon years ago (Alley, 2000a,b; Rodbell, 2000). Ultimately, these climatic events were driven by predictable orbital variations in Earth’s eccentricity, precession, and tilt that control how much solar insolation is received at various latitudes, which in turn initiate a complex, not entirely understood sequence of feedbacks within the climate system. The net effect is that at certain times, thresholds are reached which result

in the growth or decline of ice sheets and related climatic and physical–environmental changes (Raymo, 1998; Raymo *et al.*, 1998; Ruddiman, 2001).

The evolutionary role of these dramatic Quaternary climatic changes continues to engender debate (Bennett, 2004). Such repetitive climatic changes could be expected to accelerate speciation rates, because of their clear effect on geographic ranges of both plants and animals, and the consequent increased likelihood of isolating small populations in areas with new selective regimes (Dynesius and Jansson, 2000; Jansson and Dynesius, 2002). On the other hand, it is becoming increasingly apparent that the reason that geographic ranges of organisms shift with climatic changes is because species are tracking their climate space across the landscape (Graham and Grimm, 1990; Walther *et al.*, 2002; Root *et al.*, 2003; Webb III *et al.*, 2004). If this is the case, new selective regimes would not necessarily be encountered with climatic change. Furthermore, given the cyclical nature of the Quaternary climatic change, alternate expansion, contraction, and/or back-and-forth movement of geographic ranges would be expected, with the geographic isolates of one part of the climate cycle being reconnected to the main range in the following part of the cycle. In this case, any changes in gene frequencies that were induced by random drift or selection during the isolate phase might have little chance of fixation, because isolation would not be maintained for long enough periods. If this model of constant mixing within an effectively stable climate space holds true, then Quaternary speciation rates should be unremarkable relative to the rest of mammalian history, as has been argued for plants and insects (Bennett, 1990, 1997; Coope, 2004).

Here I discuss empirical studies that shed light on how Quaternary climatic changes affected speciation. I constrain the question by asking whether orbitally induced climatic variations, which cycle on time scales of between 41,000 and 100,000 years, stimulated new species to form. Studies that deal with tracing evolutionary patterns over longer or shorter time scales, or at lower (population to genes) or higher (genera and families) taxonomic scales, might arrive at different answers, but resolution between conflicting data can often be found with proper attention to geographic, temporal, and taxonomic scale. In contrast to recent similar studies (Lister, 2004), which have looked at the problem emphasizing Eurasian data, my geographic focus is North America, although I draw on comparative examples from other parts of the world. From the perspective of evolutionary biology, answering the question as I have constrained it sheds light on whether Court Jester or Red Queen models drive evolution at the Quaternary time scale at mid-latitudes of the North American continent—a place where ice-front biogeographic disruptions would have been particularly pronounced—and whether the North American data is at variance with other studies.

MATERIALS AND METHODS

If Quaternary climatic changes stimulated speciation above background levels, at least some of the following three predictions should hold true. (1) Calculated Quaternary speciation rates should exceed the average speciation rate for mammals. (2) Molecular data should show many extant sister-species to have diverged within the last 100,000 years (during the last glacial cycle), or at least within the last million years (since the shift from a 41,000-year periodicity to a 100,000-year periodicity for the climatic cycles). (3) Morphological attributes used to recognize species-level differences should demonstrate

the most change at climatic transitions. Here I review recently published information to assess whether any of the three predictions are well supported by empirical data.

It is important to note the difference between “speciation” and “population-level differentiation.” Here I consider speciation to be achieved when reproductive isolation is attained—that is, individuals from different populations can no longer produce viable offspring under natural conditions. This is essentially a biological species concept, which is appropriate here because the intent is to understand when biological entities are assured of setting off on an evolutionary trajectory that is distinct from their parent populations. Such “assurance” can only take place with irrevocable reproductive isolation. I use “population-level differentiation” or “divergence” to indicate that two populations have diverged genetically and have the potential to become different species, but still have the potential to intermingle and lose their genetic distinctiveness should the right conditions bring them back into contact. I recognize the duration of a speciation event as the amount of time that elapses from initial divergence of populations to the time when they are irrevocably reproductively isolated, following *Avise et al.* (1998).

RESULTS

Speciation Rates

Speciation rates are typically computed as a proportion of new species appearing during a given interval compared to the standing crop of all species known for the interval, ideally with standardized interval lengths and standardized sampling. However, different metrics have been applied to calculating speciation rates, producing variable results in respect to whether or not rates in Quaternary mammals are unusual. A further complication is that comparing speciation rates among fossil and modern species—as is necessary to compute differences between Quaternary mammalian rates and background rates—is not entirely straightforward, because fossil species may not be defined in the same way as extant species, and because extant species are more completely sampled than extinct ones. The main analytical bias that would be expected is that rates would be higher for Quaternary species. This is because Quaternary species include modern ones, which may be recognized by genetic or soft-tissue morphological criteria; these criteria are unavailable for most extinct species, which means that some fossil specimens that actually represent different species probably are lumped into the same species. Second, with the better sampling that characterizes Quaternary deposits, more short-lived or rare species might be known in comparison to older, less-well sampled deposits. This analytical bias means that a result that shows higher speciation rates in the Quaternary is not necessarily robust evidence that climatic change stimulated speciation, unless all of the confounding factors have been accounted for. However, given reasonable accounting for obvious sampling biases, a result that shows no increase in Quaternary speciation rates probably is fairly robust, because most biases work to inflate Quaternary rates.

Over the past two decades, various proxies for mammalian speciation rates through the North American Cenozoic have been developed (Gingerich, 1984; Barnosky, 1989; Stucky, 1990; Alroy, 1996). Except for Alroy (1996), which computed speciation rates from analysis of species lineages, those studies actually focused on genera. Using counts of genera to assess Quaternary speciation recognizes that there is a positive relationship between numbers of species and numbers of genera, which must hold true because all genera

must have at least one species, and most genera have more than one. This relationship has been discussed by previous workers (Preston, 1962a,b; Stucky, 1990). Two of the older studies (Gingerich, 1984; Stucky, 1990) suggested high origination rates in the Quaternary, and the other (Barnosky, 1989) argued for no increase in Quaternary rates.

A complicating factor in all of these older studies was the comparison of time intervals of different lengths, which can influence results (Alroy, 2000; Foote, 2000a). Gingerich's proxy for speciation rate included genera per million years (genera originating during a given time interval divided by the length of the interval), and genera per genera (originating genera per time interval divided by the total genera known for that time interval). The interval lengths were based on subdivisions of the epochs, and varied from one million years (two intervals in the Quaternary) to six million years. The taxon counts were taken from the best data that were easily obtainable at the time (Romer, 1966) but subsequently were supplanted by more detailed compilations. Barnosky used the same metrics and data as Gingerich, but attempted to make interval lengths more comparable by considering the Quaternary as one interval of two million years rather than two intervals of one million years.

Stucky's was the most rigorous of these early analyses, using taxon counts vetted from the primary literature, binning data by subdivisions of North American land mammal ages, and supplying several origination metrics. One metric attempted to standardize for unequal bin durations by deriving origination rates (Stucky's Table IV, column R_o) with the equation $N/N_o = e^{rt}$, where N is the total number of genera present in an interval, N_o is the number of genera entering the interval, e is the natural logarithm, t is the duration of the interval, and r is the rate of origination as derived from the known parameters. He also calculated the ratio of originations in an interval compared to the number of taxa entering the interval (Stucky's Table IV, column O/N_o); originations per million years (Stucky's Table IV, column O_{my}); and provided data to calculate originations per genera known within an interval (Stucky's Table IV, divide column O by column G). The derived origination rate (R_o) and originations per million years (O_{my}) suggested markedly elevated Quaternary rates, especially for Stucky's Irvingtonian 1 (approximately 750,000–1.5 million years ago), the Rancholabrean (approximately 100,000 years ago to 10,000 years ago in his usage), and the Recent (10,000 years ago to the present); the same holds true when applying the origination rate equation of Alroy (2000, p. 723) to Stucky's data.

However, the very unequal interval lengths affect these metrics, as detailed in other publications (Foote, 1999, 2000a; Alroy, 2000). The Quaternary is chopped into time intervals orders of magnitude shorter than the comparative intervals and thus would be expected to show an elevated origination rate as an analytical artifact. In this case, the analytical artifact is compounded by sampling biases. The Rancholabrean sample (thousands of localities) is orders of magnitude better than the Irvingtonian (less than 40 localities) (FAUNMAP Working Group, 1994, 1996; Bell *et al.*, 2004), and Stucky's Recent sample included living as well as fossil taxa. As Stucky pointed out, the extremely high origination rate for the Recent is largely explained by the fact that 29 extant species not known as fossils were included in the total of 117 Recent species. In effect, the sampling biases are so extreme they result in an inverse relationship between number of localities and interval length for the four Quaternary intervals that Stucky defines. That is opposite to the relationship between the number of localities and interval length for most of the North American Neogene, which approximates the linear relationship $y = 45.77x + 76.59$, $r^2 = 0.49$ (as

determined by binning Neogene data from the MIOMAP database [Carrasco *et al.* 2005] approximately as Stucky did for his data).

In view of the relative oversampling of Quaternary localities, an arguably better way to treat the data is to apply metrics that emphasize standardizing for number of samples within an interval, rather than those that emphasize correcting for bin length. This cannot be done directly with Stucky's data, but can be approximated by standardizing for numbers of taxa known in a particular bin, since numbers of taxa correlate strongly with numbers of localities (Barnosky and Carrasco, 2002). Applying such metrics completely remove the appearance of high Quaternary origination rates from Stucky's data, as illustrated by the ratios of (1) genera originating divided by genera known in an interval (Fig. 1A); and (2) originations in a given interval divided by the number of genera known from the previous interval (Fig. 1B).

The most comprehensive comparison of speciation rates of mammals through the Cenozoic was provided by Alroy and colleagues (Alroy, 2000; Alroy *et al.*, 2000), who worked around the problem of comparing unequal interval lengths by sorting taxa into bins of 1 million years through a method called appearance event ordination (Alroy, 2000). Origination rates were computed as the natural log of numbers of species at the end of an interval, divided by the number of species that were present at the start, minus the number that went extinct during the interval. The potential problem of unequal sample sizes per interval was addressed with standardized subsampling routines (Alroy, 2000). The analyses were not for speciation rate *sensu stricto*, but for origination of new "lineages," which takes into account pseudo-extinction and pseudo-origination. Because that and other nuances were applied uniformly through the entire time scale, the studies provide a good measure of how originations in the two Quaternary 1-million-year temporal bins compared with originations in the previous 1-million-year bins, reaching back to 70 million years ago. The highest origination rate (~ 1.75) for mammals was ~ 65 million years ago; the lowest (~ 0.10) was ~ 32 and ~ 20 million years ago, and Quaternary rates (~ 0.25) were very close to the mean.

In contrast, Quaternary speciation rates in Europe have been suggested to be above the background rate for Miocene speciation (Lister, 2004). The analysis involved comparing ~ 1.7 million year intervals of the Miocene to the ~ 1.8 million year interval of the Quaternary, and therefore eliminated any major biases introduced by comparing differing interval lengths. Lister calculated "relative turnover," which is the sum of first and last appearances of species within a given time interval, divided by the total number of species. The possible ratios that result range from 0, indicating no originations or extinctions in the interval, to 2, indicating that all taxa originated and went extinct within the interval. Lister found that in Italy the relative turnover for the Quaternary was close to 1.5, considerably above the mean of 0.9 for the Miocene derived from most of western Europe. He also estimated that Quaternary rates for much of Europe could be between 1.0 and 2.0, but recognized that obtaining a value much above 1.0 would assume a large but unknown proportion of species that both originated and went extinct within the Quaternary.

Relative turnover may not be a good estimator of speciation *per se*, because it conflates the separate metrics of speciation, extinction, immigration, and emigration, which have been shown in many studies to act independently and respond to different stimuli (Stucky, 1990; Foote, 2000b). For example, a relative turnover value of 0.5 could be obtained by having no species originate but half the species going extinct in an interval, by no species going

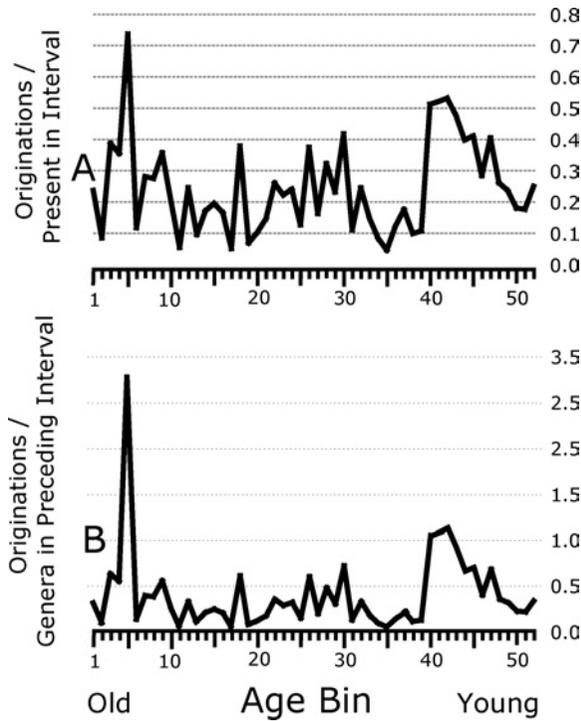


Fig. 1. Two metrics that can be used to depict the origination of genera per time period of the Cenozoic, in a way that indirectly corrects for the over-representation of Quaternary (especially Rancholabrean and Recent) localities relative to earlier Cenozoic time bins. These metrics do not correct for interval length, but doing so with these data introduces an artificial inflation of Quaternary speciation rates because so many more Quaternary localities are known, and the Quaternary time intervals are orders of magnitude shorter than any other interval. The curves are plotted from the data given in Table IV of Stucky (1990). **A**, divides Stucky's column O by his column G. **B**, plotting of results given in Stucky's column O/N_o. Age bins are subdivisions of the North American Land Mammal Ages as Stucky (1990) interpreted them; durations (in millions of years) he assigned for each are given in brackets in the list that follows. The Quaternary is composed of bins 49, 50, 51, and 52. 1-Lancian 1 [0.07]; 2-Lancian 2 [0.04]; 3-Lancian 3 [0.08]; 4-Puercan 1 [0.25]; 5-Puercan 2 [0.75]; 6-Puercan 3 [0.75]; 7-Torrejonian 1 [0.75]; 8-Torrejonian 2 [0.75]; 9-Torrejonian 3 [0.75]; 10-Tiffanian 1 [0.80]; 11-Tiffanian 2 [0.80]; 12-Tiffanian 3 [0.80]; 13-Tiffanian 4 [0.80]; 14-Tiffanian 5 [0.80]; 15-Clarkforkian 1 [0.75]; 16-Clarkforkian 2 [0.75]; 17-Clarkforkian 3 [0.75]; 18-Wasatchian 1 [1.60]; 19-Wasatchian 2 [1.50]; 20-Wasatchian 3 [1.20]; 21-Wasatchian 4 [1.00]; 22-Wasatchian 5 [0.60]; 23-Bridgerian 1 [0.50]; 24-Bridgerian 2 [1.00]; 25-Bridgerian 3 [1.00]; 26-Uintan 1 [2.00]; 27-Uintan 2 [2.00]; 28-Uintan 3 [2.00]; 29-Duchesnean 1 [3.00]; 30-Duchesnean 2 [2.00]; 31-Chadronian 37.5 [1.00]; 32-Chadronian 36.5 [1.00]; 33-Chadronian 34.5 [1.00]; 35-Chadronian 32.5 [1.00]; 36-Orellan 31.5 [1.00]; 37-Orellan 30.5 [1.00]; 38-Whitneyan 29.5 [1.00]; 39-Whitneyan 28.5 [1.00]; 40-Arikarean 1 [6.00]; 41-Arikarean 2 [3.00]; 42-Hemingfordian [3.50]; 43-Barstovian [5.00]; 44-Clarendonian [2.50]; 45-Hemphillian 1 [3.00]; 46-Hemphillian 2 [1.50]; 47-Blancan 1 [1.50]; 48-Blancan 2 [1.25]; 49-Irvingtonian 1 [0.70]; 50-Irvingtonian 2 [0.75]; 51-Rancholabrean [0.10]; 52-Recent [0.01].

extinct but half of them originating, or by one quarter of the species going extinct and one quarter originating. Moreover, Italy is a small geographic area relative to Europe as a whole. The smaller the geographic area, the higher the turnover rate might be expected to be, because local immigrations and emigrations would be counted as turnover events. Thus, the most robust comparisons of turnover rates are probably to be found in comparing geographic areas of similar size. While the relative turnover data suggest some interesting biotic events, further investigations are required to parse out the different components of the turnover rates before they can be argued to support elevated speciation.

In sum, metrics that emphasize removing the bias caused by the extremely rich sample of Quaternary mammals relative to earlier time periods show no elevation of Quaternary speciation rates. Such metrics use some combination of standardizing for sample size more heavily than they do for time, and/or they bin the Quaternary into at least million year bins, rather than subdividing it into bins that are orders of magnitude smaller than the bins for earlier Cenozoic data. Metrics that take the Quaternary sample at face value as equivalent to the pre-Quaternary sample, and standardize primarily for interval length, show greatly enhanced speciation rates for the Quaternary. This is probably an artifact that simply results from being able to temporally bracket origination events more tightly as both the completeness of the sample and the temporal resolution increase, both of which are orders of magnitude better in the last half of the Quaternary than in earlier time periods.

Molecular Studies

The majority of relevant molecular data comes from phylogeographic and related studies that focus on mitochondrial (mt) DNA (Avice *et al.*, 1998; Hewitt, 2000, 2004). By determining the sequence divergence of mtDNA between extant sister-species and populations within species, and applying standard molecular clocks, it is possible to estimate the time since two groups of interest have diverged. In turn, this allows an estimation of the minimum and maximum amount of time it takes for populations to diverge to the point where they become different species, that is, irrevocably reproductively isolated. The minimum estimate is derived from the sequence divergence observed between populations, and the maximum estimate is derived from the divergence between sister-species. Avice *et al.* (1998) applied this approach in a meta-analysis that compared divergence times for extant sister-species with divergence times for phylogroups within species. They analyzed data for 92 sister-species pairs, and 72 infraspecific phylogroups.

Given that the median duration of a mammalian species is somewhere between 2.2 and 2.6 (Alroy, 2000; Vrba and DeGusta, 2004) and 1.7 million years (Alroy, 1996, 2000; Foote and Raup, 1996), and assuming as a null model that species arise randomly through time, it would be expected that between about 35 and 53% of extant sister-species pairs would have diverged in the Quaternary (last 1.8 million years) by chance alone. We would therefore expect significantly more than 32–49 sister-species (the chance number of divergences for the longer and shorter estimates of species duration) to have diverged in the Quaternary if climatic oscillations were stimulating speciation, that is, if we are to reject the null model. The 35% estimate (32 species) is probably a better one to use, because it assumes a median species duration of 2.6 million years that is based on more refined data and equations than the 1.7-million-year estimate (Alroy, 2000). In fact, between 23 and 46 (depending on different assumptions about how to treat the divergence data) of the divergences considered

by Avise *et al.* (1998) were estimated to have occurred in the Quaternary. This may in fact slightly overestimate the number of Quaternary divergences, because Avise *et al.* (1998) rounded the beginning of the Quaternary to 2 million years (rather than 1.8 million years). However, the estimation is close enough for the purposes used here. Under an assumption of a 2.6-million-year species duration, the low end of the range of divergences (23 species) would reject the null model but would not support accelerated speciation in the Quaternary; in fact, this scenario would suggest abnormally slow speciation rates, with fewer divergences than expected (Chi-square probability = 0.049). Using the high end of the Avise *et al.* (1998) divergence range (46 species) would reject the null model and lend support to accelerated Quaternary speciation (Chi-square probability = 0.002). At least 41 divergences would be needed to maintain this support at the 0.05 alpha level. The uncertainties in the estimates of species duration and how many species actually diverged in the Quaternary (arising in part from molecular clock uncertainties) renders such evidence for accelerated speciation rates equivocal at best.

In contrast, there is convincing evidence for considerable population-level (intraspecific) divergence within the Quaternary. Of the 72 pairs of phylogroups examined, 72% of the divergences were estimated to fall within the past two million years (Avise *et al.*, 1998). Whether or not these represent accelerated rates of population-level evolution is not yet possible to determine, because we lack sufficient estimates of how long populations typically persist for both Quaternary and pre-Quaternary time, and for the “normal” amount of variation in populations through long spans of time. For the Quaternary, such estimates may eventually be forthcoming through the burgeoning field of phylochronology (Hadly, 2003; Hadly *et al.*, 2004) and other applications of ancient DNA to study fossil population structure (Hadly *et al.*, 1998, 2003; Barnes *et al.*, 2002).

Lister (2004) provides additional examples that indicate common population-level change during the Quaternary. In some cases, divergence that leads to recognition of subspecies happened within the last 10,000 years, after the last glacial advance (lemmings, moose, deer, yellow-bellied and hoary marmots). In others, divergence of subspecies magnitude took much longer, from 150,000 to 500,000 years (shrews, woodchucks, moose, red deer/wapiti). Species-level divergences that occurred in the Quaternary include *Urus maritimus* and *U. arctos* (polar and brown bears); *Lynx lynx* and *L. canadensis* (Eurasian and American lynx), and three species of *Lemmus* (lemmings). Divergence times for all of these are placed at least several hundreds of thousands of years ago (Lister, 2004). Neither the divergence of subspecies nor of species can be linked to particular climatic oscillations; thus, at present there is no way to distinguish whether the divergences are randomly distributed through Quaternary time, or cluster at times of climatic transitions.

Strong evidence for the effects of Quaternary climatic change on population-level divergence come from the global patterns revealed by phylogeographic studies (Hewitt, 2000, 2004; Lessa *et al.*, 2003). Basically, divergences are temporally shallow in temperate latitudes where the effects of climatic change and landscape modification were most pronounced as glaciers advanced and retreated (Beringia, northern Europe). In tropical (Amazonia) and refugial areas (southern Europe), population-level divergences are temporally deeper, reaching back to pre-Quaternary time in many cases.

Thus, from the molecular perspective, there seems little doubt that Quaternary climatic changes stimulate evolutionary change among populations. Despite this, estimated divergence times for sister-species do not offer strong support that the population-level

changes led to the formation of many new species. Only by using the longest reasonable estimate for the duration of a mammalian species, and the highest estimate for the number of extant sister-species that diverged during the Quaternary, can one argue that the observed number of Quaternary speciation events was higher than expected.

Morphological Changes

A direct way to test for the effects of climate change on Quaternary mammals is to trace population-level changes in local areas through times of changing climate. If the climate is forcing evolutionary change, there should be more change across climate-transition boundaries than within climatically more stable times, and the temporal sequence of observed changes should be consistent with proposed speciation models. Molecular studies have recently been applied in this way (Hadly *et al.*, 1998, 2003, 2004), but because of preservational constraints the studies have typically focused mainly on climate changes that took place within the past few thousand years. For deposits that are hundreds of thousands of years old—that is, during the time molecular data suggest most of the Quaternary species-level and population-level divergences took place—morphology must be used as a proxy for genetic change.

Requisite datasets for tracing populations at single localities are rare; one applicable site is the Porcupine Cave Pit Sequence (PCPS), Colorado (Polly, 2003; Barnosky, 2004; Barnosky and Bell, 2004; Barnosky *et al.*, 2004a,b). In that sequence of strata, sedimentary changes provide independent climatic proxies of two glacial–interglacial transitions that took place between 1,000,000 and 600,000 years ago, and thousands of fossil specimens provide a means by which to trace population-level changes in small mammals across the same time. Of particular interest is a part of the PCPS that apparently records the change from the 41,000-year-cycle of glacial–interglacial oscillations that characterized the first half of the Pleistocene to the 100,000-year-rhythm that was dominant by 600,000 years ago. Because that was one of the most unusual climatic events within the context of the Pleistocene climatic oscillations, marked by an increase in amplitude and periodicity of the glacial–interglacial cycles, one might predict the most pronounced evolutionary effects at that time, about 800,000 years ago (Vrba, 1995a,b; Dynesius and Jansson, 2000; Jansson and Dynesius, 2002; Barnosky and Bell, 2003).

Population-level changes of three taxa from the PCPS were studied in the context of interpreting effects of climatic change on evolutionary change: marmots (Polly, 2003; Barnosky *et al.*, 2004a,b); ground-squirrels (Goodwin, 2004); and sage-brush voles (Barnosky and Bell, 2003). Marmots and ground-squirrels exemplify taxa which hibernate for 8–9 months per year, and on which climate exerts a direct selective impact because winter survival is linked to temperature of the hibernacula, and to the amount of fat reserves that accumulate during the short spring/summer season, which in turn is influenced by seasonality of temperature and precipitation that controls growth of the plants on which the marmots feed. Sage-brush voles illustrate a contrasting life-history strategy. They are active year-around, with climate exerting selective pressures in part because adequate snow-cover is required in winter to insulate them as they forage subnivally, but precipitation must be in the range to promote sage-brush growth, which they use for cover and shade in the summer.

Research that focused on tracing the morphological characters that had taxonomic significance in these taxa revealed no direct correlation between climatic changes and morphologic changes in the marmots or ground-squirrels. Instead, morphological changes proceeded randomly in relation to climatic change, and in marmots, also randomly in respect to population reductions that did coincide with the most pronounced glacial–interglacial transition. The examined traits included length, width, and proportions of molars, all of which have been used to recognize taxonomic differences among species of these groups.

In contrast, significant population-level change roughly coincident with the 41,000- to 100,000-year periodicity shift is apparent for sage-brush voles. The taxonomic trait of interest is the number of triangles formed by the enamel bands on the occlusal surface of the first lower molar. At the periodicity shift, a greater proportion of the population exhibited an extra (fifth) triangle on the first molar, and the first appearance of the most derived morphotype (with six triangles) is evident. However, the morphologic shift did not play out as the origin of a new species; rather, it shifted the mean of the trait within populations, and apparently expanded the range of variation exhibited by populations, but the overall variation among populations persisted for at least 800,000 years.

Another approach to morphological study reconstructs evolution of Pleistocene populations or species in a three-dimensional space–time context, by taking into account samples from throughout a given temporal and geographic range. Such studies are scarce, because they require a particularly dense fossil record for a given taxon. At the population-level, detailed study of *Microtus pennsylvanicus* populations across the Pleistocene–Holocene boundary in Appalachia suggests that some traits may have been affected by climate change, an equal number were not, and that the traits that were affected differed from locality to locality (Barnosky, 1993). These considerations suggested that climatic changes stimulated mosaic infraspecific evolution, but would not lead to speciation.

At the species level, patterns of change that have been reported for the Quaternary are trends, exemplified by mammoths (Lister, 1993; Lister and Sher, 2001) and muskrats (Martin, 1993). Typically, such studies document that the attainment of species-level status takes several hundreds of thousands of years, that is, the accumulation of changes over multiple glacial–interglacial cycles. While it may be that the alternate contraction and expansion of geographic ranges stimulated by interglacial cycles contributes to evolution of these species, such trends do not differ in principle from some evident in pre-Quaternary taxa, for example, Eocene ungulates (Gingerich, 1985).

Vrba (1995a) explicitly attacked the question of whether Quaternary climatic change stimulated speciation in South African bovids, by examining how closely in time first appearance events through the Neogene correlated with major climatic events. Only at particularly pronounced changes in climate state—those evidenced by a change in the periodicity of climatic cycles—did she discover elevated rates of taxon first appearances. One of the periodicity shifts was the one from a 41,000–100,000 cycle that took place around 750,000 years ago and was noted above; a more pronounced effect was the shift from a 23,000–19,000-year-cycle to a 41,000-year-rhythm that took place around 2.8 million years ago (Vrba, 1995a). Thus, most of the climatic oscillations of the Quaternary did not detectably affect speciation in the groups she studied, but the unusual climatic events did.

Other research on morphologic change of mammals across climatic boundaries has concerned changes across the Pleistocene–Holocene transition some 10,000 years ago. Typically, such studies focus on recognizing the change a taxon exhibits through some wider

portion of its geographic range than a single locality. Among the taxa that have been reported to exhibit detectable morphological change at across the Pleistocene–Holocene transition are bison (McDonald, 1981; Wilson, 1996), African bovids (Peters *et al.*, 1994), jaguars (Seymour, 1993), and various rodents (Martin, 1993). In all of these cases, the reported changes were body-size reductions that were consistent with ecophenotypic change rather than with genotypic change.

DISCUSSION

It seems clear that the genetic structure of populations was affected by the last glacial advance and retreat in arctic and temperate high-latitudes, and from that it is probably safe to infer that previous glacial–interglacial cycles also stimulated genetic changes in populations inhabiting those regions. In general, divergences are deeper than the last glacial cycle in temperate regions of the northern hemisphere that were south of maximum ice advance, suggesting physical disruption of the landscape, rather than change in specific climatic parameters, was the major stimulus of population-level change (Hewitt, 2000, 2004). The tropics exhibit very deep divergences, suggesting little stimulation of evolution by Quaternary climate change (Lessa *et al.*, 2003).

From a morphological perspective, the case studies discussed above suggest that south of the ice sheet, taxonomically significant characters usually fluctuated randomly in respect to climate changes. As suggested previously (Hadly *et al.*, 2004; Hewitt, 2004), the reaction within various species was probably connected to life-history strategy, with taxa such as voles demonstrating some population-level changes in response to climatic changes, and taxa such as ground-squirrels and marmots demonstrating no effect. Where changes in taxonomically significant characters have been correlated in time with local climatic changes, the pattern seems to be one of mosaic, infraspecific evolutionary change, whereby some populations exhibit changes in one trait, others exhibit changes in a different trait, and new traits do not usually become widely distributed (Barnosky, 1993). Most of the morphological changes that have been demonstrated for the late Pleistocene–Holocene transition seem to represent ecophenotypic effects, not necessarily genetic changes.

It is not clear whether the population-level changes that are demonstrable during the Pleistocene exceeded the background rate for pre-Quaternary time, but whether or not they did, they do not seem to have led to elevated speciation rates. Only the least conservative interpretation of the sequence divergence data would suggest that more species diverged during the Quaternary than would be expected by chance, and elevated Quaternary speciation is not indicated by metrics that appropriately use the time-series of fossil data to track origination rates through the Cenozoic.

It seems unlikely that typical glacial–interglacial oscillations consistently stimulated evolution that directly led to speciation in mammals during the Quaternary. However, two lines of morphological evidence suggest that the out-of-the-ordinary climatic transition that marked the shift from 41,000- to 100,000-year glacial cycles may have been stimulated evolution for some taxa. This event took place between 700,000 and 1,000,000 years ago, and coincides with demonstrable, population-level effects in sage-brush voles (Barnosky and Bell, 2003), and potentially with a pulse of speciation in South African bovids, although the main turnover pulse for that group came with an earlier out-of-the-ordinary periodicity shift near 2.8 Ma (Vrba, 1995a). On the other hand, mtDNA divergence data (Avise *et al.*,

1998) do not seem to support a higher-than-average number of divergences beginning one million years ago, either between sister-species pairs or between infraspecific phylogroups. In fact, a majority of sister-species pairs diverged prior to 1,000,000 ago. Between 500,000 and 1,000,000 years ago, divergences are at their lowest estimated frequency for both the sister-species pairs and the infraspecific phylogroups.

The empirical evidence reviewed herein rejects the notion that orbitally regulated glacial–interglacial cycles stimulated speciation to rise above background levels during the Quaternary. However, the evidence also demonstrates that genetic and morphological effects on populations of some species coincided with some climatic oscillations, as predicted by existing models (Vrba, 1995b; Dynesius and Jansson, 2000; Jansson and Dynesius, 2002). Models that accommodate these observations are those in which species essentially track their climate space as it moves across the landscape. The “tracking” is likely accomplished through dispersal that is ultimately controlled by growth and decline of local populations. Climatic oscillations cause changes in population size in local areas; where specific climatic parameters enhance survival, populations grow and individuals disperse, and where climate becomes less favorable, populations decline. Where populations decline, they may become isolated and be subjected to new selective pressures; however, by virtue of their small size, their most likely fate is extinction. Also working against speciation is the cyclical nature of orbital climatic variation. Even if a small population persists and obtains new traits through enhanced selection and drift, its most likely fate is to be genetically reunited with parent populations within a maximum of 100,000 years. This simply may not be enough time for complete reproductive isolation to develop, except in rare cases. Similar arguments have been made from observations of plants and insects (Bennett, 1990, 1997; Coope, 2004).

Elsewhere I have argued that the cyclical climatic oscillations themselves may select against species that respond to them (Barnosky, 2001). In short, if selection at a given climatic transition stimulates transformation of a population into a new species (that is, isolation and selection cause that population to attain reproductive isolation), that new species has at most 100,000 years before it faces an equally severe climate change. If it has the capacity to withstand the first of these, it has the capacity to withstand all of similar magnitude that follow. If it cannot withstand the next oscillation and goes extinct, it will have only existed 100,000 years—a time so short that the likelihood of preservation in the fossil record or giving rise to sister-species is very small. The preservation probability is further lessened by Vrba and DeGusta’s (2004) analysis of what African fossil-mammal data say about how long it takes for a newly appearing species to become geographically widespread. Their data indicated that newly appearing mammal species start out with small geographic distributions and do not become geographically widespread until about 500,000 years later. Small geographic ranges are usually correlated with low population sizes (Brown, 1995), which translates to rare preservation as fossils.

Work on other organisms suggests that these observations from mammals may reflect a general evolutionary phenomenon. It has long been argued that Quaternary climatic changes did not stimulate speciation in plants (Bennett, 1990, 1997), and recent research continues to support that (Kadereit *et al.*, 2004; McKinnon *et al.*, 2004; Willis and Niklas, 2004). Similar conclusions have been drawn from synthetic studies of birds (Avisé *et al.*, 1998; Klicka and Zink, 1999; Zink *et al.*, 2004), fish (Avisé *et al.*, 1998), herpetofauna (Avisé *et al.*, 1998), and insects (Coope, 2004). Some species very likely did arise in the Pleistocene or Holocene, as illustrated by detailed studies of certain groups of mammals (Hosey, 1982;

Capanna *et al.*, 1996; Lister, 2004), birds (Klicka *et al.*, 1999), fish (Seehausen, 2002), and insects (Freitag, 1979; Knowles, 2000; Barraclough and Vogler, 2002). However, these cases of Pleistocene and Holocene speciation seem to be more the exception than the rule, and it has yet to be demonstrated that they indicate any deviation from normal background rates of speciation in respect to longer time spans.

CONCLUSIONS

My analysis focused on North America, but conclusions are not at odds with information emerging from other parts of the world, especially when a clear distinction is drawn between populations (which have the potential to interbreed even though they may have diverged) and species (which I recognize as reproductively isolated). The data surveyed here suggests that the cyclical climate changes of the Quaternary did not contribute to elevated speciation rates. Instead, they promoted genetic change at the population level, but the selective pressures and isolating mechanisms that went into effect at each cycle were too short-lived to lead to the extended periods of reproductive isolation that would be required for speciation. Set in the context of the Red Queen–Court Jester dichotomy, the data seem to reject the proposal that Court Jester models are routinely operative on the Quaternary time scale. Therefore, if climate is a major influence in evolution above the population level, the important climatic changes will be those that are atypical in respect to those that cause Quaternary glacial–interglacial cycles.

Examples of such potentially important climatic events are the changes in periodicity of the orbital influences that took place around one million years ago and around 2.8 million years ago. Sound theoretical arguments suggest that both could be expected to have had pronounced biotic effects (Vrba, 1995b; Dynesius and Jansson, 2000; Barnosky, 2001; Jansson and Dynesius, 2002). So far the empirical data for species turnover seem stronger for the older event than the younger one (Vrba, 1995a), but much work remains to be done in compiling and analyzing appropriate datasets from different parts of the world.

With the recent advances in building and studying databases of Cenozoic mammal occurrences on several continents (FAUNMAP Working Group, 1994; ETE, 2004; NOW, 2004; PBD, 2004; Vrba and DeGusta, 2004; Carrasco *et al.*, 2005), it is becoming more tractable to test these ideas in deeper time and over longer time scales, for example, by examining faunal response to such events as the pronounced, sudden warming event that took place near the end of the Paleocene, the dramatic cooling at the Eocene–Oligocene boundary, the late Oligocene warming, the mid-Miocene climatic optimum, and late Miocene cooling (Katz *et al.*, 1999; Zachos *et al.*, 2001; Barnosky and Carrasco, 2002). Given that the Quaternary climatic cycles seem unlikely to have been drivers of speciation, a challenge now is to use these longer-term datasets to discover whether there are other scales of climatic change that are critical to stimulating evolution. If so, it will be interesting to see whether those climate-driven evolutionary events are globally synchronous, or staggered in time because global climate changes manifest differently in different geographic settings.

ACKNOWLEDGMENTS

This research was partially supported by NSF Grant EAR-0310221. I thank Richard Stucky and John Alroy for providing information about their analyses and commenting on

the manuscript; Adrian Lister and R. Nichols for their constructive reviews; and P. D. Polly for inviting me to contribute this paper. The work benefited from discussions with Elizabeth Hadly and members of my lab group: Marc Carrasco, Edward Davis, Samantha Hopkins, Brian Kraatz, and Alan Shabel. This is University of California Museum of Paleontology Contribution no. 1864.

LITERATURE CITED

- Alley, R. B. (2000a). Ice-core evidence of abrupt climate changes. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 1331–1334.
- Alley, R. B. (2000b). The Younger Dryas cold interval as viewed from central Greenland. *Quaternary Sci. Rev.* **19**: 213–226.
- Alroy, J. (1996). Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**: 285–311.
- Alroy, J. (1998). Equilibrial diversity dynamics in North American mammals. In: *Biodiversity Dynamics: Turnover of Populations, Taxa and Communities*, M. L. McKinney and J. A. Drake, eds., pp. 232–287, Columbia University Press, New York.
- Alroy, J. (2000). New methods for quantifying macroevolutionary patterns and processes. *Paleobiology* **26**: 707–733.
- Alroy, J., Koch, P. L., and Zachos, J. C. (2000). Global climate change and North American mammalian evolution. In: *Deep Time: Paleobiology's Perspective*, D. H. Erwin and S. L. Wing, eds., pp. 259–288, Allen Press, Lawrence, Kansas.
- Awise, J. C., Walker, D., and Johns, G. C. (1998). Speciation durations and Pleistocene effects on vertebrate phylogeography. *Proc. R. Soc. Lond. B* **265**: 1707–1712.
- Barnes, I., Matheus, P., Shapiro, B., Jensen, D., and Cooper, A. (2002). Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science* **295**: 2267–2270.
- Barnosky, A. D. (1989). The late Pleistocene event as a paradigm for widespread mammal extinction. In: *Mass Extinctions: Processes and Evidence*, S. K. Donovan, ed., pp. 235–254, Belhaven Press, London.
- Barnosky, A. D. (1993). Mosaic evolution at the population level in *Microtus pennsylvanicus*. In: *Morphological Change in Quaternary Mammals of North America*, R. A. Martin and A. D. Barnosky, eds., pp. 24–59, Cambridge University Press, Cambridge.
- Barnosky, A. D. (2001). Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. *J. Vertebr. Paleontol.* **21**: 172–185.
- Barnosky, A. D. (2004). Faunal dynamics of small mammals through the Pit Sequence. In: *Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado*, A. D. Barnosky, ed., pp. 318–326, University of California Press, Berkeley.
- Barnosky, A. D., and Bell, C. J. (2003). Evolution, climatic change and species boundaries: Perspectives from tracing *Lemmys curtus* populations through time and space. *Proc. R. Soc. Lond. B* **270**: 2585–2590.
- Barnosky, A. D., and Bell, C. J. (2004). Age and correlation of key fossil sites in Porcupine Cave. In: *Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado*, A. D. Barnosky, ed., pp. 64–73, University of California Press, Berkeley.
- Barnosky, A. D., and Carrasco, M. A. (2002). Effects of Oligo–Miocene global climate changes on mammalian species richness in the northwestern quarter of the USA. *Evol. Ecol. Res.* **4**: 811–841.
- Barnosky, A. D., Bell, C. J., Emslie, S. D., Goodwin, H. T., Mead, J. I., Repenning, C. A., Scott, E., and Shabel, A. B. (2004a). Exceptional record of mid-Pleistocene vertebrates helps differentiate climatic from anthropogenic ecosystem perturbations. *Proc. Natl. Acad. Sci. U.S.A.* **101**: 9297–9302.
- Barnosky, A. D., Kaplan, M. H., and Carrasco, M. A. (2004b). Assessing the effect of middle Pleistocene climate change on *Marmota* populations from the pit locality. In: *Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado*, A. D. Barnosky, ed., pp. 332–340, University of California Press, Berkeley.
- Barraclough, T. G., and Vogler, A. P. (2002). Recent diversification rates in North American tiger beetles estimated from a dated mtDNA phylogenetic tree. *Mol. Biol. Evol.* **19**: 1706–1716.
- Barton, N. H. (2001). Speciation. *Trends Ecol. Evol.* **16**: 325.
- Bell, C. J., Lundelius, E. L., Jr., Barnosky, A. D., Graham, R. W., Lindsay, E. H., Ruez, D. R., Jr., Semken, H. A., Jr., Webb, S. D., and Zakrzewski, R. J. (2004). The Blancan, Irvingtonian, and Rancholabrean mammal ages. In: *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*, M. O. Woodburne, ed., pp. 232–314, Columbia University Press, New York.
- Bennett, K. D. (1990). Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology* **16**: 11–21.
- Bennett, K. D. (1997). *Evolution and Ecology, the Pace of Life*, Cambridge University Press, Cambridge.

- Bennett, K. D. (2004). Continuing the debate on the role of Quaternary environmental change for macroevolution. *Philos. Trans. R. Soc. Lond. B* **359**: 295–303.
- Brett, C. E., and Baird, G. C. (1995). Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. In: *New Approaches to Speciation in the Fossil Record*, D. H. E. a. R. L. Anstey, eds., pp. 285–315. Columbia University Press, New York.
- Brown, J. H. (1995). *Macroecology*, University of Chicago Press, Chicago.
- Capanna, E., Bekele, A., Capula, M., Castilia, R., Civitelli, M. V., Codjia, J. T. C., Corti, M., and Fadda, C. (1996). A multidisciplinary approach to the systematics of the genus *Arvicanthis* Lesson, 1842 (Rodentia, Murinae). *Mammalia* **60**: 677–696.
- Carrasco, M. A., Kraatz, B. P., Davis, E. B., and Barnosky, A. D. (2005). *Miocene Mammal Mapping Project (MIOMAP)*, University of California Museum of Paleontology. <http://www.ucmp.berkeley.edu/miomap/>.
- Clark, P. U., Alley, R. B., and Pollard, D. (1999). Northern hemisphere ice-sheet influences on global climate change. *Science* **286**: 1104–1111.
- Coope, G. R. (2004). Several million years of stability among insect species because of, or in spite of, Ice Age climatic instability? *Philos. Trans. R. Soc. Lond. B* **359**: 209–214.
- Coyne, J. A., and Orr, H. A. (1998). The evolutionary genetics of speciation. *Philos. Trans. R. Soc. Lond. B* **353**: 287–305.
- Dansgaard, W., Johnson, S. J., Clausen, H. B., Dahljensen, D., Gundestrup, N. S., Hammer, C. U., Hvidberg, C. C., Steffensen, J. P., Sveinbjornsdottir, A. E., Jouzel, J., and Bond, G. (1993). Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature* **364**: 218–220.
- Dynesius, M., and Jansson, R. (2000). Evolutionary consequences of changes in species' geographical ranges driven by Milankovitch climate oscillations. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 9115–9120.
- ETE. (2004). *Evolution of Terrestrial Ecosystems Database*, <http://www.nmnh.si.edu/ete/>.
- FAUNMAP Working Group. (1994). FAUNMAP: A database documenting late Quaternary distributions of mammal species in the United States. *Illinois Mus. Sci. Pap.* **25**: 1–690.
- FAUNMAP Working Group. (1996). Spatial response of mammals to the late Quaternary environmental fluctuations. *Science* **272**: 1601–1606.
- Foote, M. (1999). Morphological diversity in the evolutionary radiation of Paleozoic and Post-Paleozoic crinoids. *Paleobiology* **25**: 1–15.
- Foote, M. (2000a). Origination and extinction components of taxonomic diversity: General problems. In: *Deep Time: Paleobiology's Perspective*, D. H. Erwin and S. L. Wing, eds., Allen Press, Lawrence, Kansas.
- Foote, M. (2000b). Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology* **26**: 578–605.
- Foote, M., and Raup, D. M. (1996). Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* **22**: 121–140.
- Freitag, R. (1979). Reclassification, phylogeny, and zoogeography of the Australian species of *Cincindela* (Coleoptera, Cincindelidae). *Aust. J. Zool.* **66** (Suppl. Ser.): 1–99.
- Gavrilets, S., Li, H., and Vose, M. D. (1998). Rapid parapatric speciation on holey adaptive landscapes. *Proc. R. Soc. Lond. B* **265**: 1483–1489.
- Gingerich, P. D. (1984). Pleistocene extinctions in the context of origination–extinction equilibria in Cenozoic mammals. In: *Quaternary Extinctions: A Prehistoric Revolution*, P. S. Martin and R. G. Klein, eds., pp. 211–222, University of Arizona Press, Tucson.
- Gingerich, P. D. (1985). Species in the fossil record: Concepts, trends, and transitions. *Paleobiology* **11**: 27–41.
- Goodwin, H. T. (2004). Systematics and faunal dynamics of fossil squirrels from Porcupine Cave. In: *Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado*, A. D. Barnosky, ed., pp. 172–192, University of California Press, Berkeley.
- Graham, R. W., and Grimm, E. C. (1990). Effects of global climate change on the patterns of terrestrial biological communities. *Trends Ecol. Evol.* **5**: 289–292.
- Graham, R. W., and Lundelius, E. L., Jr. (1984). Coevolutionary disequilibrium and Pleistocene extinctions. In: *Quaternary Extinctions: A Prehistoric Revolution*, P. S. Martin and R. G. Klein, eds., pp. 223–249, University of Arizona Press, Tucson.
- Hadly, E. A. (2003). The interface of paleontology and mammalogy: Past, present, and future. *J. Mammal.* **84**: 347–353.
- Hadly, E. A., Kohn, M. H., Leonard, J. A., and Wayne, R. K. (1998). A genetic record of population isolation in pocket gophers during Holocene climatic change. *Proc. Natl. Acad. Sci. U.S.A.* **95**: 6893–6896.
- Hadly, E. A., van Tuinen, M., Chan, Y. L., and Heiman, K. (2003). Ancient DNA evidence of prolonged population persistence with negligible genetic diversity in an endemic tuco-tuco (*Ctenomys sociabilis*). *J. Mammal.* **84**: 403–417.
- Hadly, E. A., Ramakrishnan, U., Chan, Y. L., van Tuinen, M., O'Keefe, K., Spaeth, P. A., and Conroy, C. J. (2004). Genetic response to climatic change: Insights from ancient DNA and phylochronology. *Public Libr. Sci.* **2**: e290.

- Hewitt, G. M. (2000). The genetic legacy of the Quaternary ice ages. *Nature* **405**: 907–913.
- Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philos. Trans. R. Soc. Lond. B* **359**: 183–195.
- Hosey, G. R. (1982). The Bosphorus land bridge and mammal distributions in Asia-Minor and the Balkans East Europe. *Saeugetierkundliche Mitteilungen* **30**: 53–62.
- Janis, C. M. (1989). A climatic explanation for patterns of evolutionary diversity in ungulate mammals. *Palaeontology* **32**: 463–481.
- Janis, C. M. (1993). Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annu. Rev. Ecol. Syst.* **24**: 467–500.
- Janis, C. M. (1997). Ungulate teeth, diets, and climatic changes at the Eocene/Oligocene boundary. *Zoology* **100**: 203–220.
- Janis, C. M., and Wilhelm, P. B. (1993). Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. *J. Mammal. Evol.* **1**: 103–125.
- Janis, C. M., Damuth, J., and Theodor, J. M. (2000). Miocene ungulates and terrestrial primary productivity: Where have all the browsers gone? *Proc. Natl. Acad. Sci. U.S.A.* **97**: 7899–7904.
- Jansson, R., and Dynesius, M. (2002). The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. *Annu. Rev. Ecol. Syst.* **33**: 741–777.
- Kadereit, J. W., Griebeler, E. M., and Comes, H. P. (2004). Quaternary diversification in European alpine plants: Pattern and process. *Philos. Trans. R. Soc. Lond. B* **359**: 265–274.
- Katz, M. E., Pak, D. K., Dickens, G. R., and Miller, K. G. (1999). The source and fate of massive carbon input during the latest Paleocene thermal maximum. *Science* **286**: 1531–1533.
- Klicka, J., and Zink, R. M. (1999). Pleistocene effects on North American songbird evolution. *Proc. R. Soc. Lond. B* **266**: 695–700.
- Klicka, J., Zink, R. M., Barlow, J. C., McGillivray, W. B., and Doyle, T. J. (1999). Evidence supporting the recent origin and species status of the Timberline Sparrow. *Condor* **101**: 577–588.
- Knowles, L. L. (2000). Tests of Pleistocene speciation in montane grasshoppers (genus *Melanoplus*) from the sky islands of western North America. *Evolution* **54**: 1337–1348.
- Kutzbach, J., Gallimore, R., Harrison, S., Behling, P. R., and Laarif, F. (1998). Climate and biome simulations for the past 21,000 years. *Quaternary Sci. Rev.* **17**: 473–506.
- Lessa, E. P., Cook, J. A., and Patton, J. L. (2003). Genetic footprints of demographic expansion in North America, but not Amazonia, during the Late Quaternary. *Proc. Natl. Acad. Sci. U.S.A.* **100**: 10331–10334.
- Lister, A. M. (1993). Evolution of mammoths and moose: The Holarctic perspective. In: *Morphological Change in Quaternary Mammals of North America*, R. A. Martin and A. D. Barnosky, eds., pp. 178–204, Cambridge University Press, Cambridge.
- Lister, A. M. (2004). The impact of Quaternary Ice Ages on mammalian evolution. *Philos. Trans. R. Soc. Lond. B* **359**: 221–241.
- Lister, A. M., and Sher, A. V. (2001). The origin and evolution of the woolly mammoth. *Science* **294**: 1094–1097.
- Mallet, J. (2001). The speciation revolution. *J. Evol. Biol.* **14**: 887–888.
- Martin, R. A. (1993). Patterns of variation and speciation in Quaternary rodents. In: *Morphological Change in Quaternary Mammals of North America*, R. A. Martin and A. D. Barnosky, eds., pp. 226–280, Cambridge University Press, Cambridge.
- McDonald, J. N. (1981). *North American Bison—Their Classification and Evolution*, University of California Press, Berkeley.
- McKinnon, G. E., Jordan, G. J., Vaillancourt, R. E., Steane, D. A., and Potts, B. M. (2004). Glacial refugia and reticulate evolution: The case of the Tasmanian eucalypts. *Philos. Trans. R. Soc. Lond. B* **359**: 275–284.
- NOW. (2004). *Neogene of the Old World Database*, <http://www.helsinki.fi/science/now/>.
- PBD. (2004). *The Paleobiology Database*, <http://paleodb.org>.
- Peters, J., Gautier, A., Brink, J. S., and Haenen, W. (1994). Late Quaternary extinction of ungulates in sub-Saharan Africa: A reductionist's approach. *J. Archaeol. Sci.* **21**: 17–28.
- Petit, J. R., Jouzel, J., Raynaud, D., Barkov, N. I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davis, M., Delaygue, G., Delmotte, M., Kotlyakov, V. M., Legrand, M., Lipenkov, V. Y., Lorius, C., Pépin, L., Ritz, C., Saltzman, E., and Stevenard, M. (1999). Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**: 429–436.
- Polly, P. D. (2003). Paleophylogeography: The tempo of geographic differentiation in marmots (*Marmota*). *J. Mammal.* **84**: 369–384.
- Preston, F. W. (1962a). The canonical distribution of commonness and rarity, Part II. *Ecology* **43**: 410–432.
- Preston, F. W. (1962b). The canonical distribution of commonness and rarity, Part II. *Ecology* **43**: 185–215.
- Prothero, D. R. (1999). Does climatic change drive mammalian evolution? *GSA Today*: 1–7.
- Prothero, D. R., and Heaton, T. H. (1996). Faunal stability during the early Oligocene climatic crash. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**: 239–256.
- Raymo, M. E. (1997). The timing of major climate terminations. *Paleoceanography* **12**: 577–585.

- Raymo, M. E. (1998). Glacial puzzles. *Science* **281**: 1467–1468.
- Raymo, M. E., Oppo, D. W., and Curry, W. (1997). The mid-Pleistocene climate transition: A deep-sea carbon isotopic perspective. *Paleoceanography* **12**: 546–559.
- Raymo, M. E., Ganley, K., Carter, S., Oppo, D. W., and McManus, J. (1998). Millennial-scale climate instability during the early Pleistocene epoch. *Nature* **392**: 699–702.
- Rodbell, D. T. (2000). The Younger Dryas: Cold, cold everywhere? *Science* **290**: 285–286.
- Romer, A. S. (1966). *Vertebrate Paleontology*, University of Chicago Press, Chicago.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., and Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.
- Rosenzweig, M. L. (2001). Loss of speciation rate will impoverish future diversity. *Proc. Natl. Acad. Sci. U.S.A.* **98**: 5404–5410.
- Ruddiman, W. F. (2001). *Earth's Climate, Past and Future*, W. H. Freeman, New York.
- Ruddiman, W. F., Raymo, M. E., Martinson, D. G., Clement, B. M., and Backman, J. (1989). Pleistocene evolution: Northern hemisphere ice sheets and North Atlantic Ocean. *Paleoceanography* **4**: 353–412.
- Schluter, D. (2001). Ecology and the origin of species. *Trends Ecol. Evol.* **16**: 372–380.
- Schmieder, F., Von Döbeneck, T., and Bleil, U. (2000). The mid-Pleistocene climate transition as documented in the deep South Atlantic Ocean: Initiation, interim state and terminal event. *Earth Planet. Sci. Lett.* **179**: 539–549.
- Seehausen, O. (2002). Patterns in fish radiation are compatible with Pleistocene desiccation of Lake Victoria and 14,600 year history for its cichlid species flock. *Proc. R. Soc. Lond. B* **269**: 491–497.
- Seymour, K. (1993). Size change in North American Quaternary jaguars. In: *Morphological Change in Quaternary Mammals of North America*, R. A. Martin and A. D. Barnosky, eds., pp. 343–373, Cambridge University Press, Cambridge.
- Stenseth, N. C., and Maynard Smith, J. (1984). Coevolution in ecosystems: Red Queen evolution or stasis? *Evolution* **38**: 870–880.
- Stucky, R. K. (1990). Evolution of land mammal diversity in North America during the Cenozoic. *Curr. Mammal.* **2**: 375–432.
- Van Valen, L. (1973). A new evolutionary law. *Evol. Theory* **1**: 1–30.
- Via, S. (2001). Sympatric speciation in animals: The ugly duckling grows up. *Trends Ecol. Evol.* **16**: 381–390.
- Vrba, E. S. (1992). Mammals as a key to evolutionary theory. *J. Mammal.* **73**: 1–28.
- Vrba, E. S. (1993). Turnover-pulses, the Red Queen, and related topics. *Am. J. Sci.* **293-A**: 418–452.
- Vrba, E. S. (1995a). The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: *Paleoclimate and Evolution, With Emphasis on Human Origins*, E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burckle, eds., pp. 385–424, Yale University Press, New Haven, Connecticut.
- Vrba, E. S. (1995b). On the connections between paleoclimate and evolution. In: *Paleoclimate and Evolution, With Emphasis on Human Origins*, E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burckle, eds., pp. 24–45, Yale University Press, New Haven, Connecticut.
- Vrba, E. S., and DeGusta, D. (2004). Do species populations really start small? New perspectives from the Late Neogene fossil record of African mammals. *Philos. Trans. R. Soc. Lond. B* **359**: 285–293.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. (2002). Ecological responses to recent climate change. *Nature* **416**: 389–395.
- Webb III, T., Shuman, B., and Williams, J. W. (2004). Climatically forced vegetation dynamics in eastern North America during the late Quaternary Period. In: *The Quaternary Period in the United States*, A. R. Gillespie, S. C. Porter, and B. F. Atwater, eds., pp. 459–478, Elsevier, Amsterdam.
- Willis, K. J., and Niklas, K. J. (2004). The role of Quaternary environmental change in plant macroevolution: The exception or the rule? *Philos. Trans. R. Soc. Lond. B* **359**: 159–172.
- Wilson, M. C. (1996). Late Quaternary vertebrates and the opening of the ice-free corridor, with special reference to the genus *Bison*. *Quaternary Int.* **32**: 97–105.
- Wu, C.-I. (2001). The genic view of the process of speciation. *J. Evol. Biol.* **14**: 851–865.
- Zachos, J. C., Pagani, M., Sloan, L., Thomas, E., and Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**: 686–693.
- Zink, R. M., Klicka, J., and Barber, B. R. (2004). The tempo of avian diversification during the Quaternary. *Philos. Trans. R. Soc. Lond. B* **359**: 215–220.