Chapter 6
Paleoecology in an Era of Climate Change: How the Past Can Provide Insights into the Future

Melissa I. Pardi and Felisa A. Smith

> *'A nation that forgets its past has no future'*
> *Winston Churchill*

Abstract Anthropogenic climate change is the most prominent conservation issue of our time. Expectations are that the Earth's climate will warm ~2.5–6.5° within the next century. The accompanying biological consequences will no doubt be huge. How will the diversity of life on our planet respond to rapid climate change? The best way to predict the future may be to examine the past as biota have experienced numerous episodes of climate fluctuation throughout geologic time. Some of these climatic fluctuations, particularly those of the late Quaternary, have been as rapid as those anticipated by climate warming scenarios. Analysis of the paleontological record can yield valuable information on how past climate change has shaped biodiversity in the past, and provide clues for what we may expect in the future.

Keywords Climate change • Conservation • Paleoecology • Vulnerability • Adaptation • Community dynamics • *Neotoma* • Historic ecology

6.1 Introduction

Climate change is the most pressing environmental problem humans face. Despite nearly unanimous agreement that anthropogenic greenhouse emissions are the ultimate driver of this change (Oreskes 2004), governments have yet to agree on reduction and control measures. Indeed, in the 15 years since the Kyoto protocol was signed there has been little progress made towards measurable reduction in

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global emissions of greenhouse gases; in the US, emissions have actually increased 11% since 1990 (Olivier et al. 2011). Moreover, recent proposals from global powers plan to put off action until the year 2020, exacerbating the problem. The consequence of inaction is that we are now faced with the possibility of more extreme change than previously thought likely (IPCC 2007a). Model predictions had called for a 2.5–6.5°C rise in global temperature by 2100, with some of the uncertainty reflecting the timing of the onset of emission reductions (IPCC 2007a). The failure to enact controls increases the probability that actual change will be toward the larger end of this range (IPCC 2007a).

Recent studies have highlighted the seriousness and immediacy of climate change. The extent of glacial melting observed has far surpassed that predicted (Joughin et al. 2004; Rignot and Kanagaratnam 2006; Luckman et al. 2006; Howat et al. 2007). Glaciers in the Himalayas have shrunk by as much as 20% in the past 30 years (Fujita and Nuimura 2011; Scherler et al. 2011). Polar sea ice has melted at an alarming rate and the vaunted "northern passage" is now a reality. As of 2011, the strait across the North Pole was ice-free for the first time during the summer months. Warming has already lead to perceptible changes in the number of ice free days in the US (NOAA 2001, http://www.publicaffairs.noaa.egov/releases2001/jan01/noaa01008.html). These wholesale environmental changes have already led to a number of demonstrable perturbations in ecosystems (Parmesan and Yohe 2003). Not only have changes in the abundance and distribution of species been noted, but the phenology of flowering and migration has also been altered (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; Parmesan and Yohe 2003; Root et al. 2003; Grayson 2005).

Conservationists face the daunting challenge of understanding and predicting the biotic responses to climate change over a wide variety of spatial and temporal scales. This is complicated by "an uneven understanding of the interlinked temporal and spatial scales of ecosystem responses." (IPCC 2007b, pp. 214). Yet, successful mitigation and conservation efforts hinge on an understanding of likely ecological and/or evolutionary responses to climate, which include the fine details of species interactions as well as community dynamics.

Paleoecologists know that climate change is not new to the earth systems. From the snowball earth of the Proterozoic, to the thermal maximum of the Paleocene-Eocene, to the ice ages of the Pleistocene, climate has dramatically influenced life over the history of the earth. Our present interglacial, the Holocene, is the most recent interglacial in a series of glacial-interglacial cycles that began some 2.58 million years ago. Since then, biota have experienced repeated bouts of warming and cooling with ice sheets advancing and retreating on 40,000- and 100,000-year time scales. Until fairly recently the dominant view has been that these past climate changes occurred gradually in response to natural processes (Imbrie and Imbrie 1979). This made it problematic when extrapolating past ecosystem responses to climate change to the much more rapid changes associated with human global warming. However, recent paleoevidence derived from deep-sea sediments and ice cores suggest that abrupt climate change is not uncommon (Allen and Anderson

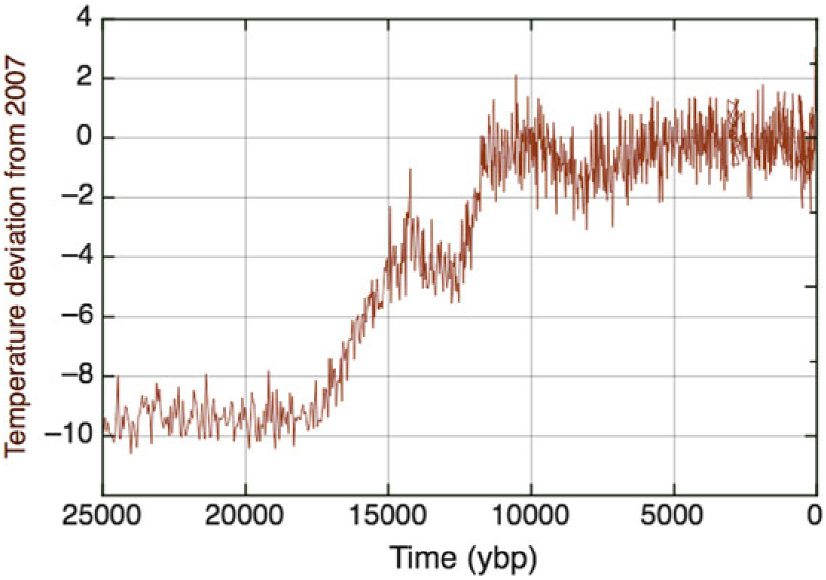

Fig. 6.1 Temperature fluctuations over the late Quaternary. Analysis of δ^{18}O from occluded air bubbles within highly resolved ice cores drilled in Greenland and the Antarctic provide a historical record of climate over the past 1 Ma. We use ice cores because of their high resolution and long temporal span; admittedly there are substantial differences in location and local climate regimes between Greenland and Antarctica and western North America where our study sites are located. However, our interest is in the relative rates of change over different time periods, not absolute temperature shifts. Data shown here were taken from the EPICA Dome C ice core (EPICA group 2004; Jouzel et al. 2007); patterns are similar with other cores

1993; Dansgaard et al. 1993; Severinghaus et al. 1998; Indermuhle et al. 1999; Alley 2000; Grootes et al. 2001; Martrat et al. 2004; Rial 2004). Indeed, highly resolved ice core records from Greenland and Antarctica reveal more than 20 abrupt shifts in the climate system during the last glacial (Fig. 6.1; Alley 2000) Each oscillation consisted of gradual cooling followed by an abrupt warming; in some cases, such as the Younger Dryas, these shifts exceeded 6–10°C over just a few decades (Alley 2000). Hence, studying the response of biota to climate shifts over the late Quaternary may be the best proxy we have for understanding future responses.

The discipline of paleoecology has become highly relevant for assessing the likely impacts of climate change on ecosystems because it works on scales that are typically larger than those used in classical ecology and more in line with that of climate (Fig. 6.2). For example, given that the average longevity of a mammalian species is around 1–2 million years (Foote and Raup 1996; Alroy 2000; Vrba and DeGusta 2004), it is clear that virtually all extant mammals have experienced multiple episodes of rapid climate change over their "lifetime". Indeed, all modern taxa in the Northern Hemisphere experienced the severe climate shifts associated with the Younger Dryas cold episode. This particularly severe event must have exerted substantial environmental selective pressure on taxa.

In this chapter, we discuss deep time patterns of biotic responses to climate change. Our emphasis is on the Cenozoic and in particular the late Quaternary

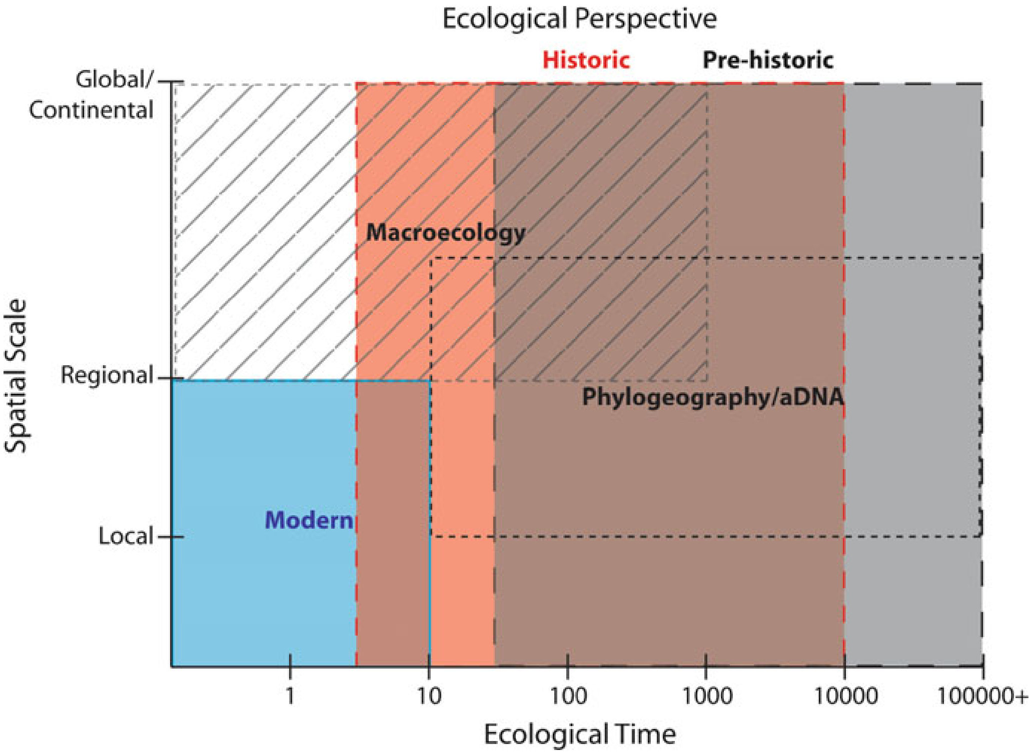

Fig. 6.2 Graphical depiction of the expected spatial and temporal scopes of modern (*blue*), historical (*red*) and paleontological (*gray*) ecological perspectives. Areas of overlap between perspectives represent areas of research that compliment each other, and are areas where modern-, historical-, and paleo-ecologists can work together. Macroecology, phylogeography, and ancient DNA (aDNA) are a few examples of sub-disciplines that overlap these ecological perspectives

because of the exceptionally well preserved and highly resolved fossil and climate record found in this Period. Recent fine-scale paleoclimatic reconstructions developed with pollen, tree ring chronologies, highly-resolved ice cores records, and other proxies have resulted in a new appreciation of how rapidly and frequently late Quaternary climate has changed (e.g., Allen and Anderson 1993; Dansgaard et al. 1993; Bond and Lotti 1995; Dahl-Jensen et al. 1998; Bond et al. 1999; Alley 2000). Thus, the past 40,000 years is arguably the best proxy we have for understanding the influence of anthropogenic climate change on organisms. We address the issue of how resilient ecosystems and species are to climate change. We characterize "resilience" as the ability of ecosystems to "absorb disturbances while retaining the same basic structure and ways of functioning, the capacity for self-organization, and the capacity to adapt to stress and change" (IPCC 2007b, pp. 880). We provide examples of studies that document the ways that species can respond to changing environmental conditions, namely through extinction/extirpation, relocation, and adaptation. Paleoecological work has documented all three of these response types. Thus, our aim is to illustrate the utility of a deep time perspective in studies of anthropogenic climate change.

6.2 Extinction/Extirpation

How resilient *are* ecosystems to environmental change? Critical to this issue is the question of what makes a species vulnerable to extinction, and it is one of the most studied questions in paleontology. It's also a question that has not been completely resolved, and most of the research in this area has focused on marine invertebrates. Still, several of the characteristics that make organisms susceptible to extinction in the fossil record may be the same characteristics predicted to increase vulnerability to future climate change. However, it should be noted that the influence of humans on the extinction process may alter the factors enhancing extinction risk (Finnegan et al. in review).

Extinction selectivity has been the focus of a tremendous amount of research on fossil marine invertebrates (Jablonski 2001, 2005, 2008; Smith and Roy 2006; Payne and Finnegan 2007; Finnegan et al. 2008; Leighton and Schneider 2008; Janevski and Baumiller 2009; Roy et al. 2009). In large part, this is because the marine fossil record is far more complete both in sampling and duration than the terrestrial record. Sepkoski (1992) was the first to assemble a large paleontological database of marine taxa to examine biodiversity over the Phanerozoic; after his death these efforts were expanded and refined (Alroy et al. 2001, 2008; Peters 2004). Such data have allowed examination of patterns of origination and speciation over geologic time. Much focus has gone into characterizing whether extinction risk is dependent on the intensity of extinction; that is, is a mass extinction fundamentally different from background events? This is relevant to anthropogenic climate change, because it is widely believed that this change will herald a sixth mass extinction event, distinct from others in that it is human mediated (Wake and Vrendenburg 2008; Barnosky et al. 2011).

A clear pattern that emerges from the aforementioned analyses on extinction vulnerability is that survivorship is clearly dependent on extinction intensity rather than ecology or life history. The particular traits that offer protection during background extinctions afford little protection during mass extinctions (Jablonski 2005; Payne and Finnegan 2007). For example, the geographic range of marine taxa is positively associated with survivorship during background extinctions, and this relationship is diminished during mass extinctions (Payne and Finnegan 2007). As such, mass extinction events are generally too widespread and too catastrophic to discriminate among species (Raup 1992).

During "normal" or background extinctions, however, several factors have been identified that can either enhance or reduce extinction risk. Low diversity can increase the odds of extinction. Monospecific genera tend to fare worse than more diverse genera with respect to extinctions (Janevski and Baumiller 2009). However being clustered in a clade means that you generally share many of the same traits. If that trait enhances extinction risk, then membership in a diverse clade offers little protection. Thus, even very diverse clades can become extinct at a higher rate than expected from random extinction (Janevski and Baumiller 2009). Large geographic range size also appears to promote survival at the clade level both for background and mass extinctions (Janevski and Baumiller 2009; Payne and Finnegan 2007).

For vertebrates, a common character used to predict extinction risk is body size (Cardillo 2003; Jones et al. 2003; Cardillo et al. 2008). Body size matters because it places constraints on many physiological and ecological traits (Peters 1983; Calder 1983; Brown et al. 2004). For example, the diversity and structure of small mammal montane communities was influenced by climate change more strongly than large-bodied taxa at glacial-interglacial transitions throughout the Pleistocene (Barnosky et al. 2004). Similarly, climate and habitat change at the end of the last glacial has caused modern communities to be relatively less diverse than those recorded from the region before the glacial (Blois et al. 2010).

Extinction risk does not appear to be random, even with regard to mass extinctions (Payne and Finnegan 2007; Janevski and Baumiller 2009). While climate change will affect species globally, regional impacts will be variable, and we can reasonably expect certain taxa to fare better than others based on pre-adaptive traits and their ecology. For example, studies on droughts from past interglacial lacustrine deposits support the prediction that the North American southwest will become more arid with anthropogenic climate change (IPCC 2007b) Huge swaths of forest have burned in recent fires connected to drought. These stands are expected to never return to their pre-burn state, but be replaced with different species (Margolis et al. 2011). Such an ecological filter would open up niches to pre-adapted species, and shape future habitats, speciation patterns, and diversity. Such rapid reorganizations from perturbations have been postulated as one of the reasons that extinctions get so bad (Erwin 2001). This is troubling if, in fact, we are going through a sixth mass extinction.

Ecological filters do not have the same effects across lineages. Whereas climate variability throughout the late Quaternary altered mammal communities substantially (Barnosky et al. 2004; Blois et al. 2010), insect faunas were not impacted in the same way. Indeed, extinction rates in insect faunas have remained relatively low, and species and communities remained fairly constant over the last million years (Coope and Wilkins 1994). Plants also exhibit distinctive patterns brought about by ecological filters. For example, during the Paleocene/Eocene warming, North American paratropical plant communities exhibited only minor changes in diversity (Harrington 2001). Similarly, abrupt climate change during the Pleistocene/Holocene transition did not induce broad plant extinctions in North America, but rather, community assemblages shifted rapidly in response (Jackson and Overpeck 2000; Davis and Shaw 2001; Williams et al. 2001; Williams and Jackson 2007; Shuman et al. 2009). The persistence of plant species during dynamic climate shifts of the late Quaternary occurred through a combination of migration and adaptation (Davis and Shaw 2001).

Ecological filters cull certain taxa, but provide opportunities for diversification and speciation in other lineages. Pre-adaptation for new climate regimes can enable a species to expand into vacated niches after extinctions occur. For example, the extinction rate of horses increased to about three to four times the background level of extinction during the Hemphilian, 6.5–4.5 million years ago (Hulbert 1993).

Increased aridity reduced horse species numbers from their peak (14–20 species) during the middle Miocene, to about three species (Hulbert 1993). However, these surviving species were pre-adapted in that they exhibited extreme hypsodonty and cursorial limb morphology (Hulbert 1993). These adaptations enabled them to survive this ecological filter, and this morphology has persisted in this lineage to the present.

How did past climate change affect extinctions during the most recent deglaciation? Interestingly, the primary response for most taxa appears to be relocation rather than extinction. If we just consider North America, virtually no species under 40 kg went extinct at the end of the Pleistocene (Lyons et al. 2004); however, many species had dramatic shifts in their ranges (Graham et al. 1996; Lyons et al. 2010). Within plants, only one tree species (*Picea critchfieldii*) has been reported as becoming extinct (Jackson and Weng 1999). As a whole, floral communities underwent major range shifts (Davis 1989; Overpeck et al. 1991; Grimm and Jacobson 1992; Williams et al. 2001; Jackson and Williams 2004; Williams and Jackson 2007; Shuman et al. 2009). Although climate change at the end of the last glacial resulted in relatively fewer instances of extinction than migration, we should keep in mind that anthropogenic climate change is happening at a much faster rate than many previous climate shifts, and that it is compounded by human activities.

6.3 Relocation

Given the opportunity, organisms have a tendency to track their preferred habitat as climate changes. The responses of organisms to anthropogenic change have already been observed in many taxa (Parmesan and Yohe 2003). These responses include the poleward tracking of ranges by numerous species of alpine herbs, butterflies, and birds. Changes in phenologies by plants and insects have also been reported, leading to potential mismatches between resources and bird or butterfly migrants (Parmesan and Yohe 2003).

A focus of late Quaternary studies has been documenting range shifts of both plants and animals in response to environmental shifts (Graham et al. 1996; Jackson and Overpeck 2000; Davis and Shaw 2001; Williams and Jackson 2007; Lyons 2003; Blois et al. 2010). The development of several comprehensive databases (e.g., Graham et al. 1994; North American Pollen Database, Grimm2000) has facilitated the analysis of past biotic response to climate. FAUNMAP (http://www.museum.state.il.us/research/faunmap/) is a relational database containing detailed information on mammalian species composition, geological age, and stratigraphy for over 2,900 late Quaternary localities across the United States (Graham et al. 1996). It has been used to examine changes in the distribution of individual species as well as entire community assemblages (Graham et al. 1996; Pardi and Graham in prep). Also of great importance has been the development of various palynological databases, particularly the North American Pollen Database (NAPD) (Grimm 2000, http://www.museum.state.il.us/research/napd/), which includes data from over 800 Quaternary sites across North America. These databases can now be accessed jointly through the Neotoma Paleoecology Database (Neotoma Paleoecology Database 2011, http://www.neotomadb.org). These archives have been instrumental in housing data used to describe Quaternary shifts in floras and faunas (Grimm and Jacobson 1992; Graham et al. 1996; Williams et al. 2001; Williams and Jackson 2007).

Mammal occurrences from the FAUNMAP database are detailed enough that shifts in species ranges can be calculated for various windows of time during the last glacial. For example, range shifts of North American mammals during transitions between pre-glacial, glacial, Holocene, and modern time slices have been examined (Lyons et al. 2010). The difference in range size between the times analyzed and the direction of range centroid movement were then related to ecological parameters. Lyons et al. (2010) compared directional changes in range movement between extinct and extant taxa. Interestingly, there was no distinction found between the direction of range shifts of extinct animals and survivors of the end Pleistocene extinction. There was, however, a weak relationship between the magnitude of the distance moved and body size, with larger mammals exhibiting significantly larger shifts.

Geographic location seems to be important with regard to range changes. During late Quaternary climate change western species consistently moved shorter distances than species in the east, regardless of body size or ecological affinity (Lyons et al. 2010). The implication is that a species living in an area of greater topographic relief does not need to shift its range very much to accommodate climate change. Additionally, mountain ranges may serve as barriers to migration. The results of this study suggest that ecological traits of mammals have a limited impact on a species' capacity to relocate itself in response to climate.

Predicting the movement of montane species in response to climate change will be important for the conservation of those species, particularly those that are already restricted to higher elevations. With increased warming, these taxa will become highly susceptible to local extirpations as habitable areas on mountaintops shrink.

Recent preliminary work of small mammal faunas from cave assemblages in the Black Hills of South Dakota are producing important taxa for understanding the structure and spatiotemporal dynamics of late Pleistocene Northern Great Plains and montane communities (Pardi 2010; Pardi and Graham in prep). These ongoing excavations are producing a mix of plains, boreal forest, and tundra species from the last 20,000 years. Dating of dental elements of specific taxa from various stratigraphic horizons has provided preliminary patterns of the local extirpation of the genus *Dicrostonyx* (collared lemming) around 17,000 year BP, the arrival and loss of the genus *Myodes* (red-backed vole) from lower elevations in the Black Hills around 13,300 year BP, and the arrival of closed environment taxa resembling the morphology of *Microtus ochrogaster* (prairie vole) around 9,500 year BP. Each of these taxa cluster around distinct time intervals, suggesting transitions from one fauna type to the next, as would be expected from progressive climate warming at the end of the Pleistocene (Fig. 6.3). Additional radiocarbon dating of these and other species are expected to clarify this pattern.

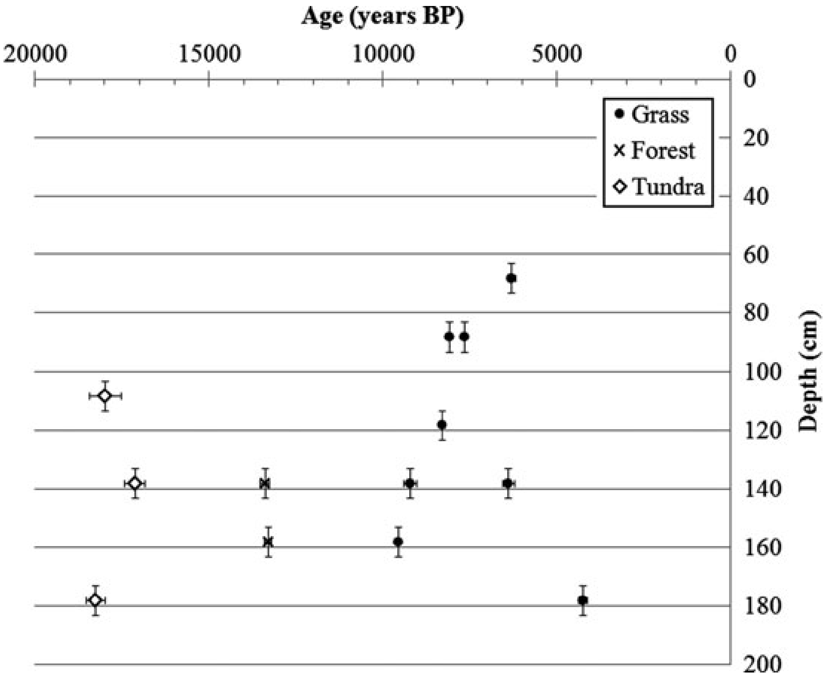

Fig. 6.3 Preliminary pattern of succession of a late Pleistocene fauna from the Black Hills of South Dakota. AMS 14C dates were obtained from individual teeth of tundra (*Dicrostonyx* sp.), closed forest (*Myodes* sp.), and open environment (*Microtus* cf. *ochrogaster*) species from throughout the cave excavation. Overlap of ages within excavation levels indicate significant mixing of strata; however, by dating individual specimens from various levels and stratigraphic types, we have estimated the time intervals of persistence for these taxa. Future dating will refine these ranges for these and other species (Pardi 2010; Pardi and Graham in prep.) Radiocarbon dates were calibrated using Calib 5.0 (Reimer et al. 2004). Median calibrated ages are reported, ± 2 s.d.

Records from the last glacial and the early Holocene are particularly valuable because they allow movements to be observed over long periods of time at the species, population, and community levels. One of the results coming out of recent work on late Quaternary biotas is that species and communities tend to behave in a Gleasonian, or individualistic, manner (Graham et al. 1996; Graham 2005; Semken et al. 2010; Williams et al. 2001; Blois et al. 2010), and that organisms have responded to climate change through both complex species interactions and interacting with their physical environment (Gleason 1926). This contrasts from the more deterministic Clementsian view of succession, where successive communities are very predictable after disturbances (Clements 1916).

It has been suggested that new non-analogue communities have the potential to emerge with future climate change (Jackson and Overpeck 2000; Williams et al. 2001; Graham 2005; Williams and Jackson 2007). A non-analogue association is the past contemporaneous occurrence of species that are geographically isolated from each other in modern faunas. Late Pleistocene faunas from across North America are more taxonomically diverse than Holocene faunas, and many contain non-analogue associations (Graham et al. 1996; Graham 2005; Blois et al. 2010;

Semken et al. 2010; Stafford et al. 2011). Some of these associations occur as a result of taphonomic mixing, but several of these associations have been verified through accelerator mass spectroscopy (AMS) ^{14}C dating (Semken et al. 2010; Stafford et al. 2011). Non-analogue faunas have also been verified on other northern hemisphere continents (Stafford et al. 2011).

If late Pleistocene faunal communities were diverse and novel, it follows that vegetation communities may have been different as well (Graham and Mead 1987; Graham and Grimm 1990; Blois et al. 2010), and non-analogues have indeed been observed in plant communities (Jackson and Overpeck 2000; Williams et al. 2001; Williams and Jackson 2007). Unlike mammal communities, which are simply defined by the co-occurrence of non-analogue species, non-analogue floras are usually defined by the percent composition of different taxa in pollen spectra, often at the genus level. These assemblages are indicative of individualistic responses to, presumably, novel climates (Williams et al. 2001; Williams and Jackson 2007). Interestingly, non-analogue floras and faunas disappear synchronously with the end Pleistocene megafauna extinction, and vertebrate community diversity also decreases after this time (Graham 2005; Blois et al. 2010). The grazing of very large megaherbivores could have kept habitats more open and increased local and regional diversity; however this does not explain non-analogue plant assemblages outright, and the existence of non-analogue climates provides a complimentary explanation (Jackson and Overpeck 2000; Williams et al. 2001).

Dispersal of plants is fundamentally different from that of animals. Range shifts occur through a combination of colonization by propagules and local extirpations, rather than the actual movement of individuals. Can the fossil record tell us how fast plants can respond to rapid climate change? The warming at the end of the Younger Dryas cold interval (~11.5 kyp) occurred extremely quickly, perhaps as quickly as a few decades (Severinghaus et al. 1998; Alley 2000). As measured from Greenland, local temperatures increased by as much as 5–10°C over this brief time (Severinghaus et al. 1998; Alley 2000). In response, there were biome-scale changes in vegetation communities in North America (Overpeck et al. 1991; Shuman et al. 2005, 2009). Dissimilarity analyses of pollen spectra from the northeastern United States show major turnovers in the composition of forests, with the crippling decline of spruce (*Picea*) (Shuman et al. 2009). The spruce species *Picea critchfieldii* was widespread through eastern North America, but went extinct during the last deglaciation (Jackson and Weng 1999).

Rapid climate change during the transition out of the last glacial period influenced the trajectory of Holocene biotic communities. In the northeastern United States, spruce never returned to its pre-Younger Dryas extent, and was replaced almost entirely by pine (*Pinus*), hemlock (*Tsuga*), and beech (*Fagus*) (Shuman et al. 2009). The characteristically diverse spruce and hardwood forests from this region were reduced to marginal environments by the end of the Pleistocene (Jacobson et al. 1987).

The Younger Dryas is, temporally, the closest analog we have to modern anthropogenic climate change. Shifts in community composition such as those seen at the end of this event should evoke a sense of urgency with the prospect of anthropogenically induced climate change. The paleontological record indicates that major community turnovers over large geographic scales can happen within a single human lifetime.

6.4 Adaptation

Most studies of extant organisms overlook the possibility of adaptation to climate change. In general, the assumption appears to be that climate shifts will occur too rapidly for species to respond (Huntly 2007). Yet the literature is replete with examples of rapid evolutionary response to strong selection (Thompson 1998). Is it possible for organisms to adapt? What evidence exists that organisms have adapted to past climate changes? While the paleontological record has always yielded a record of the dynamic nature of animal and plant distributions, more recent work is providing important insights into the evolutionary capability of organisms to respond to environmental perturbations. The most likely and perhaps the easiest way for organisms to adapt to climate change are through changes in body size.

Why body size? Scientists have long known that how animals interact with their environment is strongly influenced by their body size; temperature directly influences the energetic relationships and physiology of animals (Calder 1983; Peters 1983). Indeed, for many taxa the relationship between body mass and temperature is so predictable over time and space that the pattern is known as Bergmann's rule (Bergmann 1847; Rensch 1938; Mayr 1956, 1963). Bergmann's rule is the idea that, for a broadly distributed genus, those species of larger size are found in colder environments, and those of smaller size are found in warmer areas (Bergmann 1849). Although originally formulated in terms of species within a genus, it also holds in terms of populations within a widely dispersed species. The pattern was named after the German physiologist, Carl Bergmann, who was among the first to propose it (Mayr 1956). Among contemporary animals it appears to be generally valid for a solid majority of vertebrates, including birds and mammals; interestingly, it also holds for numerous species of ectotherms, including bacteria, protests, plants, insects, marine organisms, and turtles (Ashton et al. 2000; Millien et al. 2006). In addition to the spatial gradient, Bergmann's rule has been observed in populations over historical and evolutionary time when exposed to varying environmental conditions (Davis 1977, 1981; Purdue 1980; Smith et al. 1995; Smith and Betancourt 1998).

The mechanism underlying Bergmann's rule is often interpreted as a direct physiological response to temperature (Mayr 1956, 1963). As organisms increase in body mass, surface area increases more slowly than volume (surface area α length^2, versus volume α length^3), such that the ratio of S to A scales as $\sim V^{2/3}$. Because heat loss is proportional to surface area, this means that larger animals lose less heat per unit mass than smaller conspecifics. Thus, they have an advantage under cold environmental conditions. Conversely, smaller animals have a greater surface to volume ratio and are more capable of dissipating heat under thermally stressful warm conditions. However, this explanation is not universally accepted (Millien et al. 2006); and several other causal mechanisms have also been proposed for the ecogeographic pattern. These include those invoking gradients in productivity, life history characteristics, development rates and other factors related to thermal characteristics of the environment.

Regardless, Bergmann's rule illustrates the strong selection imposed on organisms by their environment and the potential ability of species to adapt to fluctuating abiotic conditions over evolutionary time. Clearly, the occupation of novel environments, or abrupt shifts in climate or environmental conditions, must radically alter energetic allocation between the essential activities of survival, reproduction and growth. Consequently, it has been argued that morphological shifts in body mass may be the simplest way for animals to respond to environmental change (Barnosky et al. 2003). Whether morphological changes are largely phenotypic or genetically based has not been determined, but considering the high heritability of body mass in many animals, it is likely a combination of the two (Smith et al. 2004).

Paleoecologists have recently been able to document the ability of mammals to adapt to late Quaternary climate perturbations. For example, we have examined the morphological response of *Neotoma* (woodrats) to late Quaternary climate across their geographic range in a number of studies (e.g., Smith et al. 1995; Smith and Betancourt 1998, 2003, 2006; Smith et al. 2009). Our work uses ancient woodrat middens (debris piles) as a source of primary fossil data. Woodrats, or packrats as they are sometimes called, are just that: collectors of material that they deposit in large conspicuous debris piles blocking the entrances to their houses. The materials found within typically consist of plant fragments, fecal pellets, small rocks and other materials gathered by woodrats and held together in an indurated conglomerate of evaporated urine. Middens provide both protection against predators and insulation against thermal extremes. When dens are constructed in rocky outcrops, the protected middens can be preserved for thousands of years and are easily radiocarbon-dated. All woodrat species construct middens to some degree; thus, paleomiddens are ubiquitous across mountainous regions of western North America. A single mountain transect may contain dozens of discrete middens spanning some 30,000 years or more (e.g., Lyford et al. 2003; Jackson et al. 2005; Smith et al. 2009).

Of interest here is that each paleomidden provides an estimate of the population body mass at the time it was deposited. The most abundant component within a midden are fossilized woodrat fecal pellets; the width of these scales robustly with body mass (Smith et al. 1995). Thus, by measuring the hundreds to thousands of pellets within a distinct radiocarbon-dated sample, we can obtain an estimate of the body size of the population of woodrats that produced it. Each midden record also yields plant macrofossils and so we can also obtain information on diet and vegetation communities. In short, we can characterize the morphological and genetic responses (via aDNA) of populations to climate fluctuations over thousands of years.

Our studies clearly demonstrate that woodrat populations readily adapted to the climate changes of the late Quaternary climate by changing body size (Smith et al. 1995; Smith and Betancourt 1998, 2003, 2006; Smith et al. 2009). In most instances, the response is perfectly predicted by Bergmann's rule; woodrats were larger during cold temporal intervals, and smaller during warmer episodes. Interestingly, we find remarkably consistent patterns across the entire distributional range likely reflecting the geographic similarity of environmental fluctuations (Smith and Betancourt 2006). The patterns are somewhat more complicated at geographic range boundaries where animals approach the limit of their physiological and ecological thermal tolerances (Smith and Betancourt 2003). At range edges, high elevation populations demonstrate the predicted Bergmann's rule response, while lower elevation populations are sometimes extirpated if the severity of the environmental shifts is too great.

A strong advantage to working with late Quaternary materials is that study species are extant. Thus, it becomes possible to integrate paleontological work with lab and field studies on contemporary animals. Such work suggests physiological constraints are likely the proximate mechanism underlying the Bergmann's rule cline. Maximum, minimum and lethal environmental temperatures all significantly scale inversely with body mass (Brown 1968; Brown and Lee 1969; Smith et al. 1995; Smith and Charnov 2001). For this small rodent genus, at least, body mass is highly sensitive to temperature. We also know that much of the variation in body size is likely heritable; broad sense heritability estimates exceed 0.8 (Smith and Betancourt 2006).

More recently, we have been able to characterize environmental thresholds that lead to adaption versus extirpation of species. For the past 5 years, we have been investigating the response of *Neotoma* to late Quaternary climate change along a particularly steep elevational and environmental gradient in Death Valley National Park, California. Today, this region of North America is the hottest and driest area in the Western Hemisphere. Temperatures of over 50°C are common during the summer, and temperatures of 57°C have been recorded. However, Death Valley was not always this extreme. During the late Quaternary, for example, much of the valley was covered by pluvial Lake Manly and the climate was about 6–10°C cooler (Van Devender and Spaulding 1979; Thompson et al. 1993; Mensing 2001; Koehler et al. 2005). How did animals respond to the abrupt environmental change from a hospitable habitat to the modern hyper-arid desert?

We have now recovered and analyzed more than 100 paleomiddens from a 1,300 m elevational transect through the Grapevine Mountains on the east side of Death Valley that shed light on this question (Fig. 6.4). Our results document the changing distribution of two woodrat species over the last 32,000 years (Smith et al. 2009). One of these was a large-bodied form, *Neotoma cinerea*, typically found in cooler forested habitat; the other, a small-bodied form, *Neotoma lepida*, characteristic of the Mojave desert (Smith and Betancourt 1998). During the late Pleistocene, only the large-bodied form was present. As climate fluctuated, the animals adapted in situ. Eventually as glaciers retreated and climate warmed, populations both adapted and slowly retreated upslope. By the mid-Holocene, this species was

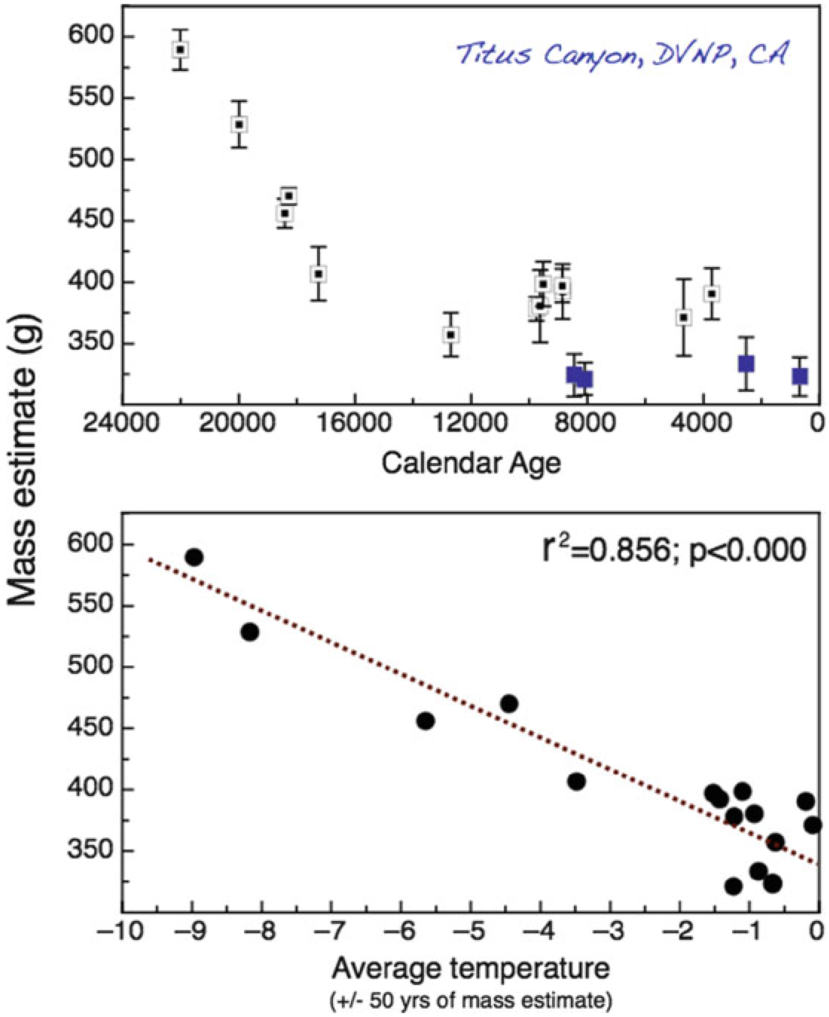

Fig. 6.4 Body mass changes over the last 25,000 years along an elevational transect in Titus Canyon, Death Valley National Park. An additional 50 paleomiddens were collected, but have not yet been radiocarbon-dated. Note the rapid dwarfing of mass that occurs at the terminal Pleistocene as ice sheet retreat and the climate rapidly warms. The relationship between body mass and the temperature at the time of midden deposition is shown in the lower panel. Temperature estimates are taken by averaging Greenland ice core estimates falling within 50 years above and below the radiocarbon date of the paleomidden. Note that the desert woodrat, *Neotoma lepida*, does not enter this canyon until the early Holocene after climate has warmed. The forest/boreal woodrat, *Neotoma cinerea*, is extirpated from this mountain range in the middle Holocene. Legend: Open squares: *Neotoma cinerea*, closed squares: *Neotoma lepida*

completely extirpated on the east side of Death Valley. Although this species was previously unknown from this region before our study, *N. cinerea* was clearly ubiquitous throughout much of the Great Basin during the Pleistocene, with distributions extending down to ~800 m elevation. Moreover, the presence of this species was apparently also tied into the displacement of juniper by almost 1,000 m relative to modern range limits (Smith et al. 2009). In contrast, the smaller-bodied form, *N. lepida*, only appeared in this area in the early Holocene. It too, adapted in situ, but slowly moved upslope in response to cave sites being abandoned by the larger-bodied species. Ultimately, *N. lepida* reached its upper distributional limit at about 1,800 m. Today, no woodrat species occupies the upper reaches of this mountain region. The results from our Death Valley project illustrate in one mountain gradient *all* the potential responses of biota to climate change: adaptation, relocation and vulnerability.

Work on other fossil populations or lineages have also demonstrated the influence of late Quaternary climate shifts on morphology. Martin and Barnosky (1993) related phyletic evolution in late Pliocene and Pleistocene musktrats (*Ondatra* sp) to climate shifts over this period America Examination of a stratigraphic section of endemic diatoms (*Stephanodiscus yellowstonensis*) from a lake in Yellowstone clearly demonstrate an abrupt morphological transition coincident with the retreat of continental glaciers; the authors attributed changes to direction selection caused by the warming climate (Theriot et al. 2006).

While studying the individualist response of species to climate changes requires analysis of single lineages, most paleoecological studies tend to be community based. This is because many fossil localities are excavations from cave or pits, which generally involves the removal and sifting of large quantities of material. These are major undertakings that can take many years to characterize. Some of the most fruitful have come from western North America, where preservation conditions are favorable. In general, an excavation results in a more restricted temporal window but yields much greater sample sizes. For example, work on Lamar Cave, a particularly rich fossil site from northern Yellowstone National Park in Montana, has yielded an exceptional record of small mammal populations over the last 3,200 years. More than 10,500 individual mammal bone fragments have been recovered and identified. This has led to number of studies that have examined species morphology, genetics, and abundance, as well as turnover in the community composition (Hadly 1996, 1997; Hadly et al. 1998). One of the most common elements recovered from Lamar Caver were pocket gophers (*Thomomys talpoides*). Analysis of size-related craniodental characters for these animals has demonstrated both morphological and ecological sensitivity of pocket gophers to the climate shifts of the terminal Holocene (Hadly 1997). Not only do gophers vary in size, decreasing during the warmer conditions of the Medieval Warm Period, but there are also significant changes in abundance related to changes within the vegetative community. Other mammals also demonstrated predictable shifts in abundance that were related to the absence or presence of preferred habitat types (Hadly 1997).

In deeper time, Porcupine Cave in the Rocky Mountains has yielded thousands of mammal fossils that date from 1 Ma to 750 Ka (Barnosky et al. 2003; Barnosky 2004; Barnosky et al. 2004). Analysis using dental morphology of the most commonly recovered mammals from this site illustrates varying adaptive responses that seem to relate to their life history. Little morphological change was observed in marmots (*Marmota* sp.) over glacial–interglacial cycles, which the authors attributed to their fossorial lifestyle. However, sagebrush vole (*Lemmiscus curtatus*), demonstrated substantial variation in dental morphology during the climate changes associated with a glacial–interglacial transition.

Paleoecology studies have also demonstrated that temperature is not always the factor that matters during climatic shifts. For example, in a study of body size variation in California ground squirrels (*Spermophilus beecheyi*), Blois et al. (2008) found that body size of populations was best explained when patterns of precipitation across the spatial gradient were also incorporated into regression models. Comparison of contemporary spatial results with fossils dating from the last glacial maximum suggested a shift towards increased precipitation in modern communities relative to the past (Blois et al. 2008). Similarly, in an early study of morphological change in carnivores, Dayan et al. (1991) found that climate factors were *not* the major determinants of body size fluctuations for many over the late Quaternary. By integrating geographic studies of modern carnivores with the fossil record, they were able to demonstrate the role of competitive interactions in influencing the body size of species. Character displacement, and not temperature or precipitation shifts, was ultimately responsible for producing the patterns observed. The importance of biotic interactions on size patterns, especially combined with climate, has been found elsewhere as well (e.g., Millien-Parra and Loreau 2000; Millien 2004; Millien and Damuth 2004).

The advent of new molecular and geologic tools is changing the field. Increasingly, paleoecologists are focusing on the influence of climate change on the genetics and biodiversity of organisms (Chan et al. 2005; Barnosky 2008). The development of ancient DNA (aDNA), despite its caveats, has revolutionized the ability to examine evolutionary processes (Higuchi et al. 1984; Willerslev et al. 2003; Briggs et al. 2007; Sampietro et al. 2007). These have led to the ability to ask directly how animals have responded to past climatic events. For example, studies of social tuco tucos from a location in South America illustrate a decrease in genetic diversity corresponding to Holocene environmental fluctuations (Chan et al. 2005). In contrast, work on pocket gophers and voles in Yellowstone National Park in Wyoming suggests genetic effects may depend on the ecology of species (Hadly 1996, 1999). While pocket gophers show a decline in genetic diversity during the Medieval Warm Period, voles increase in genetic diversity over this same time period. Other work on aDNA illustrates genetic turnover that is apparently coincident with habitat change. For example, analysis of aDNA from brown bears (*Ursus arctos*) in Beringia suggests population turnover from 60 to 14 ka (Barnes et al. 2002). Similar results are shown for muskox in northern latitudes (MacPhee et al. 2005). As techniques improve and especially, as the resolution of data increases, the integration of aDNA and phylogenetic studies is likely to be of considerable importance towards understanding how animals adapt to shifting environmental conditions.

6.5 Concluding Remarks

The field of paleoecology has been revolutionized in the past few decades by implementing cutting edge technology and techniques that have been “borrowed” from other disciplines. Stable isotopes and dental microwear have been used to tease apart ancient food webs and trophic interactions (Koch et al. 1997; Koch 1998;

MacFadden 2008; DeSantis et al. 2009; Feranec et al. 2010). Sophisticated community models have been used to look at the timing of extinction events with probable causes (Alroy 2001). Radiocarbon dating has so improved in the past decade that past population dynamics can be correlated with very small changes in past climate (Stafford et al. 1991; Stafford et al. 2011). The recent advent of macroecology also provides "a geographic and historical perspective" that may help us understand the likely effects of anthropogenic warming. As an alternative to experimental ecological research, macroecology has been remarkably successful at illuminating large-scale spatial and statistical patterns (Smith et al. 2008). Macroecology has increasingly been effectively used in climate change research (Fisher and Frank 2004; Gaston 2004; Kerr et al. 2007; Kuhn et al. 2008; Pautasso 2007; Tittensor et al. 2007; Webb et al. 2007; White and Kerr 2007; Wilson et al. 2008). Such studies have provided valuable insights into how species are influenced by climate. Less well incorporated thus far, however, is the second perspective, that of time. Macroecology and paleoecology share a lot of common ground, and it is with regard to this historical perspective that paleoecology can greatly contribute (Lyons and Smith 2010).

Future anthropogenic climate change is expected to happen at a rate much faster than most changes over earth history. With the compounding effects of human activities, earth's biota is heading into uncharted territory. Conservationists face the daunting task of trying to predict the actions that would best mediate changes to ecosystems. The window of opportunity to stave off climate change is shrinking (IPCC 2007a), and biotic consequences appear to be imminent. Our best bet is to try and implement conservation efforts synchronously with climate change to help preserve our current biodiversity. The paleoecological literature can provide important insights into patterns of past extinction vulnerability, adaptation, and community dynamics as related to climate change. Paleoecology is an important compliment to current conservation efforts, because of the temporal perspective it provides. To paraphrase Winston Churchill, paleoecology may be the key to the future.

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