



Impacts of climate change on species, populations and communities: palaeobiogeographical insights and frontiers

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Abstract: Understanding climate change and its potential impact on species, populations and communities is one of the most pressing questions of twenty-first-century conservation planning. Palaeobiogeographers working on Cenozoic fossil records and other lines of evidence are producing important insights into the naturally dynamic nature of climate and the equally dynamic response of species, populations and communities. Climatic variations ranging in length from multimillennia to decades run throughout the palaeo-records of the Quaternary and earlier Cenozoic and have been shown to have had impacts ranging from changes in the genetic structure and morphology of individual species, population sizes and distributions, community composition to large-scale biodiversity gradients. The biogeographical impacts of climate change may be due directly to the effects of alterations in temperature and moisture on species, or they may arise due to changes in factors

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such as disturbance regimes. Much of the recent progress in the application of palaeobiogeography to issues of climate change and its impacts can be attributed to developments along a number of still advancing methodological frontiers. These include increasingly finely resolved chronological resolution, more refined atmosphere-biosphere modelling, new biological and chemical techniques in reconstructing past species distributions, the development of large and readily accessible geo-referenced databases of biogeographical and climatic information, and new approaches in fossil morphological analysis and new molecular DNA techniques.

Key words: Cenozoic, climate change, dendrochronology, DNA, palaeobiogeography, palaeolimnology, palynology, vertebrate palaeontology.

I Introduction

The fundamental aim of biogeography is to document the distribution of species over space and time and understand the factors influencing those distributions. These factors can be considered to act on both ecological scales that produce changes in the population sizes and geographical distributions of species, and on evolutionary scales that drive processes such as natural selection and speciation. Palaeobiogeographers working over the Cenozoic Era (past 65 million years) have largely worked on the Quaternary Period (the past 2 to 2.5 million years) and have typically focused upon the impact of climatic fluctuations on plant and animal distributions. It is undoubted that the profound climatic changes that mark the Quaternary have left an imprint on modern-day biota through impacts on species distributions, evolution and extinction. The biogeographer, ecologist or evolutionary biologist who neglects to consider the impact of Quaternary climatic changes on present-day biota does so at their peril.

Cenozoic biogeography, and Quaternary palaeobiogeography in particular, has an increasingly important relevance as humans attempt to manage the impacts of anthropogenic habitat fragmentation and other landscape changes while also trying to anticipate and mitigate the effects of greenhouse warming. The climatic changes of the Quaternary are arguably the best analogues we have for understanding how ongoing climate changes will influence organisms in the future.

This article presents brief synopses of some of the exciting frontier areas in which Cenozoic palaeobiogeography, and Quaternary palaeobiogeography especially, is being used to address fundamental biogeographical questions. Limitations of space make it impossible to cover all of the notable work being done throughout Cenozoic biogeography. The sections that follow provide selected examples of how rapidly developing palaeoenvironmental proxies, extensive geo-referenced data sets, increasingly sophisticated modelling approaches and closer integration with palaeoclimatological research are advancing Quaternary palaeobiogeographical research. The objectives of the studies reviewed here include the traditional goals of documenting changing distributions and understanding the causes of those changes, but also extend beyond this. The ways in which palaeobiogeography can provide insights into questions such as meta-population and community dynamics or the underlying controls of large-scale species diversity gradients are also considered. Finally, examples of the increasing focus of Quaternary palaeobiogeography on the fundamental question of evolutionary biology related to the morphological and genetic response of species to climatic change are presented.

II Reconstructing changing species distributions and population sizes using palaeolimnological records

Biogeographical research is predicated upon reliable evidence of the past distributions

and population sizes of species. One of the greatest challenges faced in the growing field of limnological research, particularly in view of recent climatic and environmental change, is the lack of long-term biomonitoring to provide such data. Fortunately, lake sediments often archive a remarkably broad and constantly growing list of morphological (eg, diatom valves, invertebrate body parts, resting stages) and biogeochemical (eg, pigments) markers that can be used to reconstruct past lake biota (Smol *et al.*, 2001a; 2001b). Ongoing research using molecular and DNA approaches are now also augmenting palaeolimnological interpretations. From these proxy data, palaeolimnologists can reconstruct past species distributions, past community composition and past limnological conditions (Smol, 2008). In many cases the lake sediments contain information on terrestrial species in the watershed as well as the limnic species. As the online archive of georeferenced palaeolimnological records (<http://www.ncdc.noaa.gov/paleo/paleolim/paleolim.html>) continues to develop and grow, biogeographical applications of such data will undoubtedly increase.

Limnic sediments provide such a powerful source of information for biogeographical research because sediments integrate information spatially and temporally from the lake system. For example, Vandekerckhove *et al.* (2005) assessed the cladoceran species richness in 88 European lakes by repeated sampling of the plankton, and compared these data to the taxa that hatched from diapausing eggs from the lakes' sediments. They found that about twice as many taxa were present in the sediments compared to the number recorded from more traditional limnological sampling programmes. Palaeolimnologists have collected samples of modern lake sediments from throughout the world to calibrate transfer functions to estimate past environmental conditions. The training sets are generally used to determine species optima for important limnological variables (eg, pH, nutrients, climate). Despite the

large number of surface sediment calibration sets now available in the palaeolimnological literature, the vast majority of the biological data contained in these training sets are still often left untapped for more detailed biological monitoring. Hence, a large volume of additional biogeographical information is contained in these data sets, which could effectively be used to evaluate many hypotheses regarding the distribution of aquatic taxa. Sampling along ecotones may be especially informative in detecting relations between climate and species distributions (eg, Heegaard *et al.*, 2006). Moreover, as sediments provide a historical record of past changes in lake communities, the effects of past environmental stressors on species distributions can be assessed (Smol, 2008). As more detailed palaeolimnological studies become available, it is also becoming possible to undertake meta-analyses on broad geographical ranges to assess, for example, the occurrence and impacts of recent climate change in circumpolar regions (Smol *et al.*, 2005). Because lake sediments archive a wide spectrum of palaeoenvironmental data, multiproxy studies offer many research opportunities (and challenges) in tracking species distributions in space and time (Birks and Birks, 2006).

Many key biogeographical questions can be assessed using palaeolimnological approaches. For example, as there was no previous evidence for the occurrence of lacustrine refuges for Antarctic invertebrates during the Last Glacial Maximum, Cromer *et al.* (2006) used a palaeolimnological approach to show that, in fact, a lacustrine glacial refugium for invertebrates did exist in Antarctica. On the other side of the globe, Willerslev *et al.* (2003) used molecular techniques on sediments from Arctic permafrost regions to show that, even in the absence of obvious macrofossils, the profiles contained DNA records of at least 19 plant taxa as well as of megafauna such as mammoth, bison and horse. Such approaches could be applied on broader spatial scales to augment

palaeontological work in these regions. Palaeolimnological approaches also offer methods to study the invasion of exotic species (Hall and Yan, 1997), as well as recent extirpations (eg, Birks, 2002).

Almost all biological palaeolimnological assessments have been based on algal and invertebrate indicators preserved in lake sediments, from which the composition of past communities can be reconstructed and hence past environmental conditions can be inferred. However, recently palaeolimnologists have combined isotope analyses of lake sediments, along with morphological indicators and other proxy data, to reconstruct past populations. Important pioneering work using this integrated approach comes from the study of anadromous sockeye salmon (*Oncorhynchus nerka*) populations. Pacific sockeye salmon play an integral role in the ecology, economy and culture of many west coast communities. Although there is little doubt that sockeye salmon populations are under stress in many parts of their range, it is difficult to assess the long-term trajectories of their spatial and temporal distributions due to the absence of reliable long-term monitoring data. For some regions, reliable records extend back to the nineteenth century, but even these important data sets do not pre-date the period of fisheries, habitat destruction and other stressors. As initially proposed by Finney *et al.* (2000; 2002), palaeolimnological analyses of sockeye salmon nursery lakes can provide important insights on past species fluctuations. Because sockeye salmon are anadromous (spend part of their lives in the ocean and in freshwaters) and most have a semelparous (spawn once in their nursery lakes and tributary streams, and then die) life cycle, palaeolimnologists can track past sockeye salmon runs by reconstructing limnological conditions in the nursery lakes where the spawning adult salmon die. In some nursery lakes, millions of salmon return annually; it is not surprising that the death of these large fish in such numbers can alter

the limnological conditions of the nursery lakes. Because sockeye salmon are high in the trophic food web, they are enriched in the stable isotope ^{15}N ; upon death of the spawning adults, this ^{15}N isotope signal is preserved in lake sediments as a proxy of past sockeye salmon abundance (Finney *et al.*, 2000). Furthermore, the decaying carcasses can add a significant nutrient fertilizing effect on the nursery lakes, which can be tracked using diatoms and other indicators (Finney *et al.*, 2000; 2002). Although a variety of factors can alter the palaeolimnological signal between sedimentary isotope and microfossil analyses (Finney *et al.*, 2000) and certain *a priori* limnological criteria must be met for the study lakes (Holtham *et al.*, 2004), the approach appears to be fairly robust in reconstructing sockeye salmon populations on a variety of temporal and spatial scales (eg, Finney *et al.*, 2000; 2002; Gregory-Eaves *et al.*, 2004; Schindler *et al.*, 2006; Selbie *et al.*, 2007).

Although less developed than the sockeye salmon work, similar palaeolimnological approaches can potentially be used to track changing distributions of other animals. For example, Arctic seabirds such as the Northern fulmar (*Fulmarus glacialis*) congregate in large nesting colonies. The guano and other orthinogenic inputs from these birds can greatly influence the limnological conditions of nearby standing waters, such as the ponds below the cliffs. Using similar approaches to those developed for tracking sockeye salmon, the marine-derived nutrients and contaminants transported by past seabird populations can potentially be inferred from the palaeolimnological records of the receiving waters (eg, Blais *et al.*, 2005).

The substantive and methodological advances in palaeolimnology over the past two decades are producing exciting opportunities both to understand the distributions of aquatic species and the functioning of lakes systems and also to provide data that can be directly relevant to resource management.

III Reconstructing long-term climate changes and plant community response using research linking palaeoecological data, palaeoclimate reconstructions and models

The role of climate change in altering the distributions of species is a core area of biogeographical research, and the palaeoecological record of responses to climate change is rich in implications for ongoing and future global climate change. Multiple, independent proxies for palaeoclimate inference are proliferating from various archives across the globe. Modelling capacity has evolved from the palaeoclimate models of the COHMAP era to earth systems models integrating the atmosphere, hydrosphere and biosphere, and dynamic ecological models are being developed. Palynological data networks now extend over the globe, and are being joined by a variety of other ecological proxies, including plant macrofossils, tree-rings, vertebrates and insects. Ability to date and correlate sediment records with precision and accuracy has also improved greatly with the development of AMS dating and refinement of ^{14}C -calendar-year calibrations. These advances are leading in turn to rapid, even revolutionary, advances in understanding of ecological responses to climate changes of various rates, magnitudes and types.

Twenty years ago, efforts focused on comparing palaeoecological data derived from fossil pollen records and palaeoclimate model output, to validate and parameterize the climate models. However, climate and earth systems models are now being linked with palynological and other data at scales ranging from local to global to test ecological and biogeographical hypotheses. The large networks of georeferenced pollen records available through the various continental pollen databases (<http://www.ncdc.noaa.gov/paleo/pollen.html>) greatly help to facilitate such efforts, as do continental databases for other data types.

For example, palynological records show that vegetation with no modern compositional analogues occurred throughout the continental interior of North America and Beringia during the last deglaciation (Jackson and Williams, 2004). These inferences are corroborated by plant-macrofossil data (eg, Jackson and Williams, 2004; Edwards *et al.*, 2005) and faunal records (eg, Stafford *et al.*, 1999). Analyses of palaeoclimate simulations indicate that the contemporary climates also lacked modern analogues (Williams *et al.*, 2001). Lateglacial climates were substantially more seasonal than today, leading to unusual combinations of species and regional dominance of species that are now scarce (Williams and Jackson, 2007). The appearance and disappearance of climates and communities has important implications for future global climate change – we face risks of severe disruption of existing communities and emergence of new communities that are difficult to predict because they will be unlike any existing today (Williams and Jackson, 2007; Williams *et al.*, 2007). The risks and consequences of novel and disappearing climates might have gone unrecognized in the absence of palaeoecological and palaeoclimatic records of the phenomena.

The last deglaciation was accompanied in northern Europe and Atlantic North America by a 1200-year excursion towards colder conditions. Onset and termination of the Younger Dryas Event (YDE; 12,800–11,600 cal yr BP) were abrupt, occurring within a few decades in many regions. The magnitude of the YDE is well characterized for many regions, providing case studies in ecological response to abrupt climate change. In maritime Canada, fossil pollen records indicate that the rapid cooling led to replacement of spruce/birch (*Picea/Betula*) forest by tundra woodland, while rapid warming at the end of the YDE resulted in development of temperate forest (Levesque *et al.*, 1994; Mayle and Cwynar, 1995).

Records from Europe and eastern North America and other regions indicate that ecological responses to the rapid changes of the YDE were also rapid, occurring within decades (Birks and Ammann, 2000; Shuman *et al.*, 2002; Williams *et al.*, 2002).

These rapid responses to YDE climate changes are attributable to differential demographic responses of species within regions (eg, climate-related mortality of incumbent dominants, accompanied by increased recruitment of other species in the region), which can play out at timescales of years to decades. Whether biogeographical adjustments were rapid enough to track the climate changes of the YDE remains an open question. Birks and Birks (2008) provide evidence for a multicentury lag in the geographical-range response of *Betula pubescens* in northern Europe following termination of the Younger Dryas. Under future climate change, ecological responses will be rapid owing to mortality of many incumbents followed by opportunistic recruitment of other species, native or exotic. However, migration lags of the magnitude suggested by Birks and Birks (2008) would impart a high degree of uncertainty on model predictions of future community composition, and also suggest substantial extinction risk for many species (Davis and Zabiniski, 1992; Williams *et al.*, 2007). At least one major plant-species extinction occurred during a period bracketing the YDE (Jackson and Weng, 1999), and North American megafaunal extinctions are concentrated within that same lateglacial period (Barnosky *et al.*, 2004). Human hunting may have played an important role in the latter.

Responses to low-frequency Holocene climate change have been studied from both site-based and large-scale synoptic perspectives. Although climate-model results have been traditionally used, independent palaeoclimate proxies are playing increasingly important roles. Networks of millennial-scale lake-level records have been developed over much of the Northern Hemisphere and are available online (<http://www.ncdc.noaa.gov/paleo/lakelevel.html>).

Stable-isotope analyses of lake-sediment constituents are providing direct evidence of changes in temperature, evapotranspiration and precipitation. In New England, these records confirm that large-scale vegetational changes, including succession of various forest dominants and immigration of new tree species, were ultimately under climatic control (Shuman *et al.*, 2004). European lake-level records are also providing evidence for climatic control of Holocene vegetation dynamics (Magny *et al.*, 2001; 2003). Broader synoptic networks of these and other palaeoclimate proxies should provide detailed understanding of vegetational development over much of the globe. Palaeolimnological studies often reveal lake responses to climate change (see previous section), and can be profitably integrated with terrestrial palaeoecological records to reveal vegetational responses to climate change (eg, Clark *et al.*, 2002; Brown *et al.*, 2005).

Additional opportunities are arising as new archives and proxies are developed and applied, particularly at submillennial timescales. Ombrotrophic peatlands, for example, are yielding sensitive late-Holocene palaeoclimatic records with subcentennial resolution in cool, humid regions of Europe and North America (Mauquoy *et al.*, 2002; Charman *et al.*, 2006; Booth *et al.*, 2006). These records are helping to link vegetation changes with climate change. For example, in the central Great Lakes region of North America, a series of multidecadal droughts during a transition from wet to dry conditions led to regional decreases of beech (*Fagus*) populations, increases of white pine (*Pinus strobus*) and increases in fire occurrence (Booth and Jackson, 2003).

Tree-ring records provide opportunities for nearly seamless linkage of long-term ecological, palaeoecological and palaeoclimatic records with shorter-term events that have occurred over the past few centuries (Swetnam *et al.*, 1999). For example, late-Holocene expansion of the northern range of piñon (*Pinus edulis*) is well documented

from fossil packrat middens and population demography, and dendroclimatological records indicates that the invasion was paced by precipitation variability (Gray *et al.*, 2006). Dendroecological and palaeoecological studies of the past thousand years indicate the important role of multidecadal climate variability in governing species range dynamics and stand structure (Swetnam and Betancourt, 1998; Brown and Wu, 2005; Gray *et al.*, 2006), and provide some indications of the potential complexity of ecological responses to future climate change.

Research opportunities will continue to unfold as palaeoclimate proxies are further developed and refined, new archives are exploited and palaeoclimatological and palaeoecological data sets are used in coordinated fashion. Multiple proxies from single archives (eg, lake or peatland sediments) will refine palaeoclimate inferences, distinguishing among seasonal temperature, precipitation and evapotranspiration. Application of ecological simulation models and dynamic vegetation models (eg, Tinner and Lotter, 2006) will provide tests of the dynamic responses of vegetation to climate changes. Collaborations among palaeoecologists, palaeoclimatologists and ecologists should lead to reciprocal hypothesis generation and testing. Palaeoecological studies, for example, can suggest mechanistic hypotheses concerning range limits that can be tested experimentally in field or laboratory.

Although climate has been recognized as a determinant of the distribution and abundance of species for more than two centuries, most evidence has come from spatial correspondence between biogeographical patterns and climatic gradients. The ecological, biogeographical and palaeoclimatic history of the past 25,000 years, however, provides the strongest and most direct evidence available for the role of climate in biogeography. Examination of that history is not only vital for understanding fundamental aspects of ecology and biogeography, it is also critical for anticipating what lies ahead as the earth

enters a period of rapid climate change. From no-analogue communities to species migration to population extirpation to altered disturbance regimes, these studies are invaluable for management and policy in a world of change (Jackson, 2007).

IV Reconstructing short-term climate variations, disturbance harmonization and vegetation impacts using dendrochronology and other high-resolution palaeoclimatic records

Over the past 100 years biogeographers have also been cognizant of the importance of disturbances such as fire or wind throw on vegetation composition, demographics and the spatial structure (patchiness) of landscapes and species distributions. The degree of habitat diversity in the environment and patchiness of species distributions has important impacts on dispersal, gene flow, speciation and biodiversity and lies at the heart of metapopulation theories (eg, Young *et al.*, 1996; Hanski, 1999; Fahrig, 2003). As palaeoclimatic research tools have become more sophisticated and as large spatial arrays of palaeoclimatic sites have been developed it has become increasingly clear that the climatic variability over the past 100 years (the time period for which instrumental meteorological records are widely available) often does not represent the full range of short- to medium-term climatic changes that can occur. Such variations in climate can have durations of years to decades to centuries. Furthermore, variations in climate may affect very large areas, and through climatic teleconnections they may even be expressed simultaneously in widely separated regions. New research is showing how climatic events can in effect 'synchronize' or 'harmonize' ecosystem properties such as forest stand age and structure over wide areas through their influence on the disturbance region and mortality-recruitment patterns. The degree of overall habitat diversity or the distance between members of metapopulations associated with particular stages of succession would be

lower in climatically synchronized systems where many of the disturbance-induced patches were roughly the same age.

Widely felt climatic variations may in some cases be periodic to semi-periodic, such as El Niño–Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) variations in which recurrent changes in ocean conditions produce episodes of increased or decreased drought in specific geographical areas. They may be stochastic events triggered by variations in insolation or volcanic activity, such as the Medieval Climate Anomaly (MCA) and Little Ice Age (LIA) (Crowley, 2000). Understanding these variations in climate and their role in ecosystem structuring is of particularly critical importance today as populations become increasingly fragmented and we look to ‘natural’ examples of patchy distributions to understand the ecological and evolutionary impacts of fragmentation. Unless we understand and account for the impacts of natural climatic variability and their potentially pervasive impact on ecosystems we will have difficulty in detecting or planning for the impacts of anticipated global warming or conserving species in increasingly fragmented and human-impacted landscapes.

Rapidly developing palaeoenvironmental tools and geographically extensive databases are allowing for the direct comparison of short- to medium-term climatic shifts with changes in features such as disturbance regime or species distributions. The International Tree-ring Data Bank (<http://www.ncdc.noaa.gov/paleo/treering.html>), the North American Drought Variability database (<http://www.ncdc.noaa.gov/paleo/pdsi.html>) and the more recently developed International Multiproxy Fire Paleofire Database (<http://www.ncdc.noaa.gov/paleo/impd/paleofire.html>) provide researchers the ready opportunity to explore the relationships between short- to medium-term climatic variations and features such as drought and fire at a variety of spatial scales. These studies are finding striking geographically extensive correspondences. In

addition to allowing for improved description of past climatic variations and their biogeographical impacts, newly developing palaeoclimatic and palaeoceanographic data sets and models are allowing identification of the causes of short- to medium-term climatic variations. Some particularly well-studied examples of both short- and medium-term climatic variations and their impacts in structuring vegetation over large areas are provided by the history of variations in ENSO and the PDO, and the climatic changes MCA and the LIA.

Positive phases of the ENSO system (El Niño events) are typified by warm water in the eastern equatorial Pacific that produces increased precipitation in adjacent portions of South America and in the American Southwest. The negative phases (La Niña events) are associated with cool eastern Pacific waters and dry conditions in adjacent South America and the American Southwest. El Niño and La Niña events have an irregular recurrence interval of about 2–7 years and typically persist for 12–24 months (Philander, 1990; Trenberth, 1997). ENSO events can impact plant populations in a number of ways, including influencing growth rates, flowering and fruiting behaviour, abundance of pathogens and seed predators and fire regimes.

ENSO conditions in the eastern equatorial Pacific can be reconstructed back centuries or more from historical records, palaeoceanographic records and moisture-sensitive tree-ring records from ENSO-impacted regions (eg. Quinn and Neal, 1992; Dunbar *et al.*, 1994; Villalba, 1994). In areas where trees experience moisture stress, dendroclimatological records can be used to reconstruct the impacts of changes in ENSO while dendrochronological analyses of fire scars and stand histories can provide records of the responses of fire regime and recruitment. Important pioneering work on the large-scale ENSO–fire relations using dendrochronology was done by Swetnam and Betancourt (1990). An excellent example

of the expansion of such work comes from Kitzberger *et al.* (2001). They analysed historical climatological and fire records from the southwestern United States and the Patagonia region of Argentina, which extend back to the early twentieth century. They combined these observational records with dendrochronological fire-scar records extending back to the mid-seventeenth century. Both Patagonia and the Southwest are centres of action for the response of precipitation to shifts in ENSO. Kitzberger *et al.* (2001) found that both regions shared similar relationships to ENSO since the mid-seventeenth century (Figure 1). Major fire years tended to follow switches from El Niño to La Niña conditions. The authors surmised that increased plant productivity due to higher precipitation during El Niño events produced increased loading of fine fuels. A closely following switch to drier La Niña conditions desiccated these fuels and produced conditions promoting increased fires. Thus, fires were particularly frequent and extensive when there was a strong development of El Niños during the period prior to AD 1780 (Figure 1). A period of decreased fire occurrence in both regions took place during the period AD ~1780–1830 and appears to coincide with decreased amplitude and/or the frequency of El Niño events (Figure 1). Interestingly, there is evidence from the southwestern United States that this shift to decreased fire frequency prompted a surge in successful recruitment and survival for cohorts established during the closing period of the high El Niño activity (Figure 1). Trees established in the many sites created by fires during this time experienced relaxed fire regime during the subsequent period of decreased El Niño activity and still make up a large component of existing stands. The shifting intensity of ENSO that occurred up to hundreds of years ago may be considered still to leave an imprint on forest stand age and structure over a wide area (eg, Betancourt *et al.*, 1993).

In a recent study further north in North America, Schoennagel *et al.* (2005) used tree-ring records from subalpine fir (*Abies lasiocarpa*) stands in the Rocky Mountains from Colorado to Alberta, Canada, to produce a fire record back to the eighteenth century. They found a slightly more complex relationship between ENSO, fire and forest dynamics. In their study, they determined that the PDO, which varies on a bi-decadal to multi-decadal timeframe (eg, Biondi *et al.*, 2001; D'Arrigo *et al.*, 2001; Gedalof and Smith, 2001; Gedalof *et al.*, 2002; MacDonald and Case, 2005), was also important in producing periods of enhanced fire occurrence. Unlike the Southwest, positive ENSO conditions and positive phases of the PDO (warm waters in the eastern equatorial and northeastern Pacific) produce dry conditions in the northern Rockies. Accordingly, Schoennagel *et al.* (2005) found that in the northern Rockies large fire episodes corresponded to periods when El Niño events were linked with positive PDO conditions. In contrast, in the southern Rockies they found that ~70% of large fires burned during La Niña events that coincided with negative phases of the PDO. Further north still, Fauria and Johnson (2007) reported a relationship between changes in the ENSO and PDO regimes, prolonged droughts and increased fires in the boreal forest of Alaska and Canada. While in the Pacific Northwest, work by Hessl *et al.* (2004) has linked large-scale fire behaviour to the PDO. It is clear that in western North America the control exerted by ENSO and PDO variations on fire serves to harmonize stand age and structure of fire-induced patches over very large areas.

With some notable exceptions (eg, Swetnam, 1993) tree-ring records of past fire frequency and stand dynamics typically only extend back several centuries. Charcoal preserved in lake sediments can produce high-resolution records of fire extending back millennia (Whitlock and Larsen, 2001). In western North America a number of such

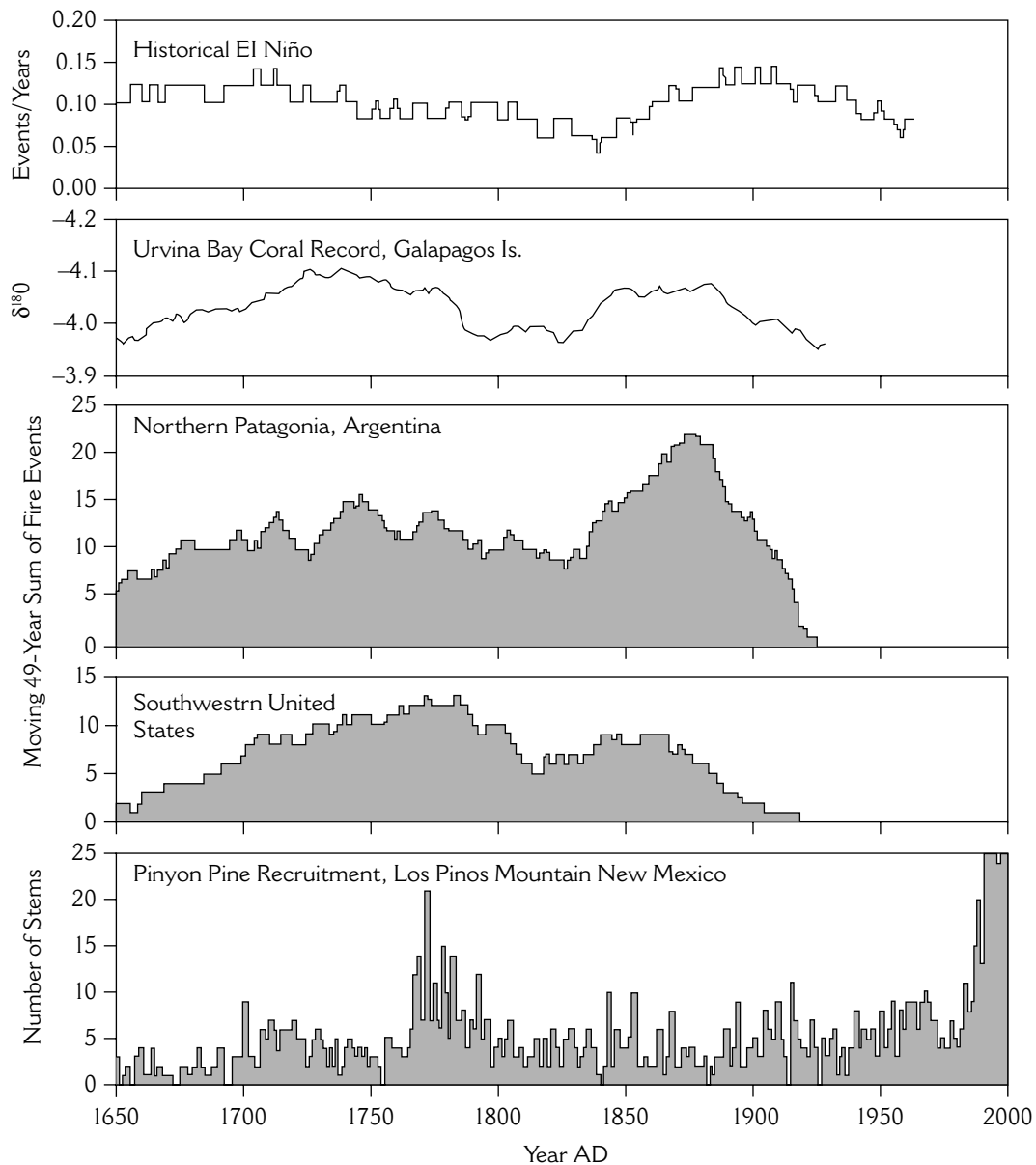


Figure 1 Evidence of the role of ENSO in the large-scale and long-distance harmonization of disturbance regimes and patch ages in Patagonia and the Southwest of the USA. The top two panels present a historical reconstruction of moderate to very strong El Niño events from archival records (Quinn and Neal, 1992) and a $\delta^{18}\text{O}$ record of ENSO-related central Pacific upwelling (more strongly negative values represent increased ENSO strength) near the Galapagos Islands (Dunbar *et al.*, 1994). The middle two panels depict the timing of widespread fires in Patagonia and the southwestern USA (smoothed with 49-year window) (Kitzberger *et al.*, 2001). The above evidence was originally collated by Kitzberger *et al.* (2001). The bottom panel depicts pinyon pine (*Pinus edulis*) stand ages from New Mexico (Betancourt *et al.*, 1993)

records document a period of high fire frequency during the MCA period of AD ~900–1300 (Figure 2). The MCA is associated with dry conditions evident in tree-ring records, plant macrofossil records, sand-dune records and other sources of palaeoenvironmental evidence from throughout southwestern North America (Cooke *et al.*, 2004). In addition to greater aridity, there is evidence of higher temperatures and higher tree-lines in the west during this period (eg, Millar *et al.*, 2006). A maximum in aridity and fire activity appears to have occurred in the twelfth century (Figure 2). It is undoubted that an event such as this would have had a significant impact on forest stand age and structure throughout the region.

Advances in climate modelling and in the development of palaeoclimatological records are now allowing the linking of aridity in southwestern North America with potential driving mechanisms related to ocean response to radiative forcing (MacDonald and Case, 2005; Mann *et al.*, 2005; Herweijer *et al.*, 2006; MacDonald *et al.*, 2007b; 2008). During the twelfth century there was a natural increase in insolation that coincided with a decrease in volcanic activity (Figure 2). This produced increased radiative forcing that according to climate model results and palaeodata could have produced a cooling of the eastern Pacific and generating prolonged La Niña-like conditions and a sustained negative state of the PDO (Figure 2). The changes in insolation, volcanic activity and ocean temperatures during the twelfth century correspond to prolonged drought across a wide stretch of southwestern North America (Figure 3) and peaks in fire frequency throughout the region. This past relationship between positive radiative forcing, North American drought and fire behaviour is particularly troubling given the current increases in radiative forcing due to greenhouse gases (MacDonald *et al.*, 2008).

The impact of drought on fire regime is not the only means by which climatic variations can lead to widespread harmonization of

ecosystems. Another interesting example arises from the northern tree-line zone. Following the MCA there was a period of general Northern Hemisphere cooling (the LIA) that was particularly marked from the sixteenth to the nineteenth centuries (Figure 4). Cooling during the LIA appears to have been a result of decreased insolation and increased volcanic activity (Crowley, 2000) (Figures 2 and 3). Stand-age analysis from sites across northern Eurasia and from North America show a similar pattern of northern tree-line response to the LIA (eg, MacDonald *et al.*, 2007a; Payette *et al.*, 2007). Mortality increased and recruitment decreased during periods of particularly cold conditions. The most recent such event, during the nineteenth century, is particularly well represented in many records (Figure 4). In northern Eurasia, dendrochronologically dated and radiocarbon dated specimens of wood from sites which lie today beyond the modern tree-line show that during the warmer MCA forest extended slightly beyond its present limits (MacDonald *et al.*, 2007a). Despite the recruitment during the relatively warm twentieth century, the forest has not yet completely recovered to its former extent in these far northern sites. The same observation has been made in northeastern Canada (Payette *et al.*, 2007). In the case of the northern tree-line, widespread changes in temperature appear to have been capable of producing equally widespread changes in forest age structure through their impact on mortality and recruitment.

The examples above provide a glimpse into a rapidly amassing database of studies that demonstrate how ecosystem demographics and structure over large regions can exhibit harmonic properties in response short- to medium-term climatic variations. There may be much less randomness in disturbance regimes and patch development over large areas than would otherwise be expected and this presents important implications for everything from metapopulation-based theories of dispersal, gene flow and evolution,

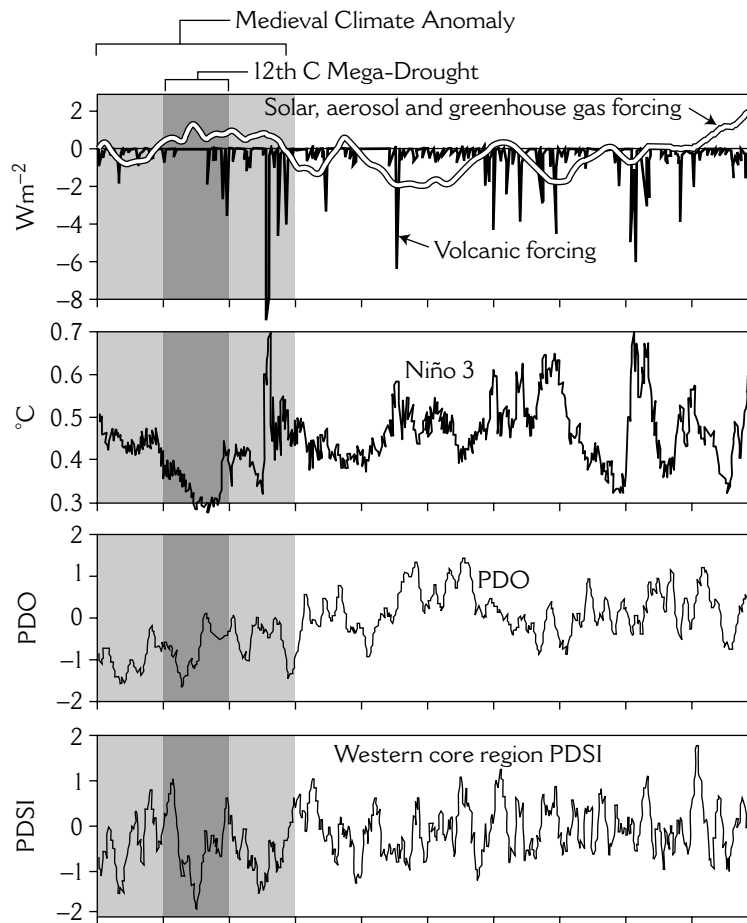


Figure 2 Evidence of the linkage between radiative forcing (increased insolation and decreased volcanic activity) during the mid-twelfth century, eastern Pacific Ocean cooling and resulting prolonged western North American drought and increased fire frequency/severity that presumably would have led to widespread development of fire-generated patches of similar age

Source: The evidence for radiative forcing is from Crowley (2000). The modelled cooling in the Niño 3 region of the eastern equatorial Pacific is from Mann *et al.* (2005). The reconstruction of the Pacific Decadal Oscillation (PDO) is from MacDonald and Case (2005). The reconstruction of increased drought severity (Palmer Drought Severity Index, or PDSI) for the core area of the twelfth-century drought from the southwestern interior of Canada to northwestern Mexico is from tree-rings (data from Cook *et al.*, 2004, and World Data Center for Paleoclimatology). Negative PDSI values indicate arid conditions. The giant sequoia (*Sequoiadendron giganteum*) fire-scar records from California are from Swetnam (1993). The lake sediment charcoal records from California, Idaho and Wyoming are from Mohr *et al.* (2000), Brunelle and Whitlock (2003) and Millspaugh *et al.* (2000). The fire records were originally collated by Cook *et al.* (2004).

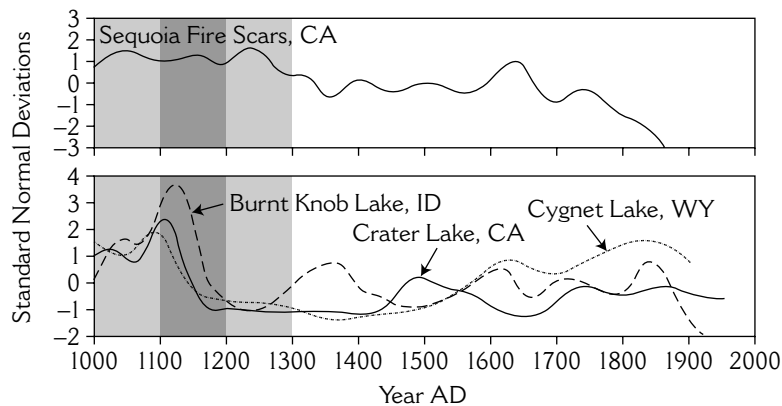


Figure 2 (continued)

to understanding species diversity, to forest management and conservation strategies in such harmonized patchy environments.

V Climate change and Cenozoic biodiversity analysed through the use of palynological records

Understanding the relationship between biological diversity and environmental factors (eg, climate, topography, area) is a core question in biogeography and has traditionally focused on using spatial data sets reflecting contemporary conditions. The majority of the research has centred on understanding the relationship between climatic parameters and diversity and in particular the relationship between diversity, available water and energy. In general, a linear relationship between precipitation and richness has been demonstrated for low latitudes, and a combined water-energy relationship with parabolic relationship between richness and energy demonstrated for mid- to high latitudes (Hawkins *et al.*, 2003; Field *et al.*, 2005) (Figure 4).

Given the large number of modern spatial data sets available, why do we need fossil records to understand what controls diversity? One of the key reasons is because the spatial records represent only a single snapshot in time. It is not possible therefore to determine

if and how diversity relationships change over multiple cycles of climate change. Fossil pollen data sets have long been used by biogeographers to examine past distribution of plant species and changes in abundance through time. When changes in energy and precipitation have been considered alongside these data the focus has tended to be upon how plant communities responded to climate change in terms of phenomena such as migration, competition and compositional change (eg, MacDonald *et al.*, 1993; Davis and Shaw, 2001; Williams and Jackson, 2007) or simply the use of the fossil record to estimate palaeoclimate (eg, Seppa *et al.*, 2004). In contrast, the fossil record has rarely been used to assess the relative influence of different climatic variables on taxonomic richness through time (Willis *et al.*, 2007). It has been predicted, however, that orbitally forced climate change on Milankovitch timescales would have had resulted in a reduction in diversity resulting from changes in geographical distributions and local extinctions (Bennett, 1997; Dynesius and Jansson, 2000). Palynological records linked with palaeoclimatic information provide an ideal means to test such hypotheses.

A number of techniques can be used to examine the relationship between diversity and time in the palaeorecord – particularly

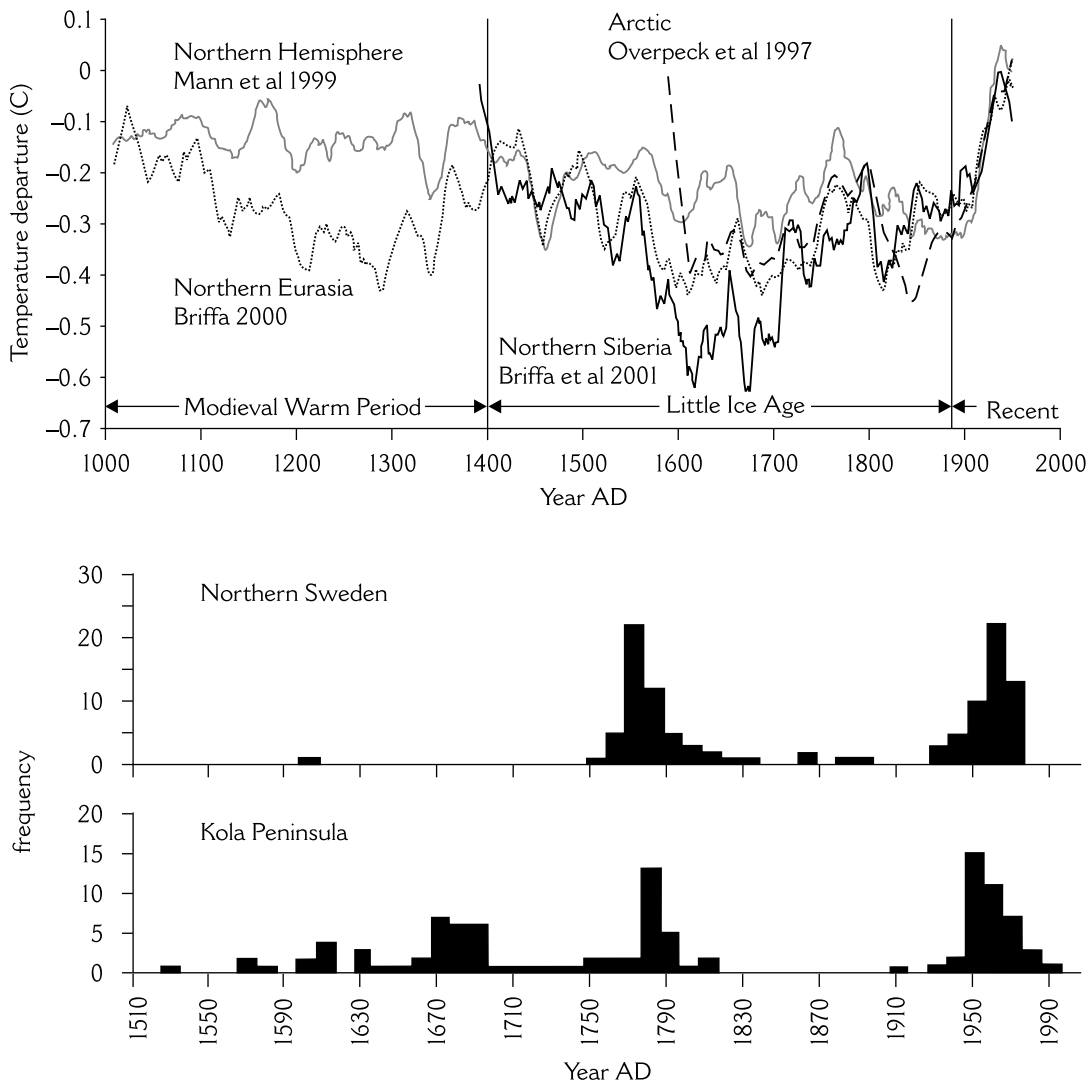


Figure 3 Evidence for harmonized response to large-scale temperature variations evident by Little Ice Age mortality and recruitment failure and twentieth-century increased recruitment for tree-line pine (*Pinus sylvestris*) and larch (*Larix dahurica*) in northern Europe and Asia

Source: Northern Hemisphere temperature is from Mann *et al.* (1999), Arctic from Overpeck *et al.* (1997) and northern Eurasian from Briffa and Osborn (1999) and Briffa (2000). Recruitment data are from *P. sylvestris* at the tree-line in northern Sweden from Zackrisson *et al.* (1995). *P. sylvestris* recruitment at the tree-line on the Kola Peninsula of northern Russia is from Gervais and MacDonald (2000). *L. dahurica* establishment (living lowland tree establishment) and establishment and mortality (dead upland trees) at a tree-line site near the Lena River delta in northeastern Siberia are from MacDonald *et al.* (1998).

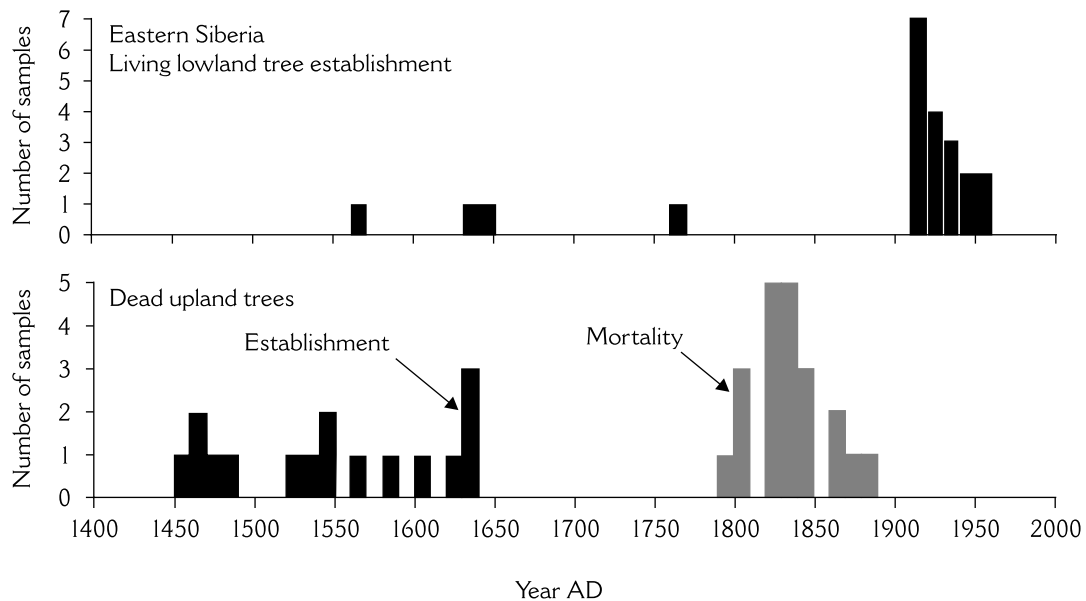


Figure 3 (continued)

fossil pollen records. These techniques include the examination of total taxonomic richness through time using rarefaction analysis (Birks and Line, 1992), examination of differences in diversity between temporally spaced samples using rates-of-change analysis (Bennett and Humphry, 1995) and examination of taxonomic turnover in the data set – both enabling taxonomic turnover calculations between and within data sets (Birks, 2007). A particular advantage of fossil pollen records is that they can span the Quaternary and extend well into earlier, but comparable and informative times of the earlier Cenozoic.

Whenever assessing diversity through time there are two key questions that need to be addressed. First, how representative are diversity fossil records of true diversity around a site (Odgaard, 1999)? Second, how do you account for the temporal autocorrelation in a sample? A number of recent studies have now indicated that in fossil assemblages the number of higher taxa provides a good predictor of species richness within local assemblages (Enquist *et al.*, 2002), and the

results from the taxonomic richness can be treated as a minimum estimate of total species richness (Weng *et al.*, 2007). Also there are now a number of numerical methods (eg, generalized Least Squares; Venables and Ripley, 2002) that can take account of temporal autocorrelation.

So what have been the main trends in diversity through time in response to climate change? What has been the main driving mechanism determining diversity – is it water, energy or does some other variable better account for changes? In order to assess the relationship between diversity and climate change it is necessary to have independent proxies for temperature and energy. There are now good palaeoclimatic reconstructions for water and temperature (energy) spanning at least the past 50 Ma (million years) and several studies have now started to examine the relationships between diversity and the reconstructed climate change over this timescale. These are revealing some interesting trends.

A study using the fossil record to examine the plant diversity in the tropics between the past

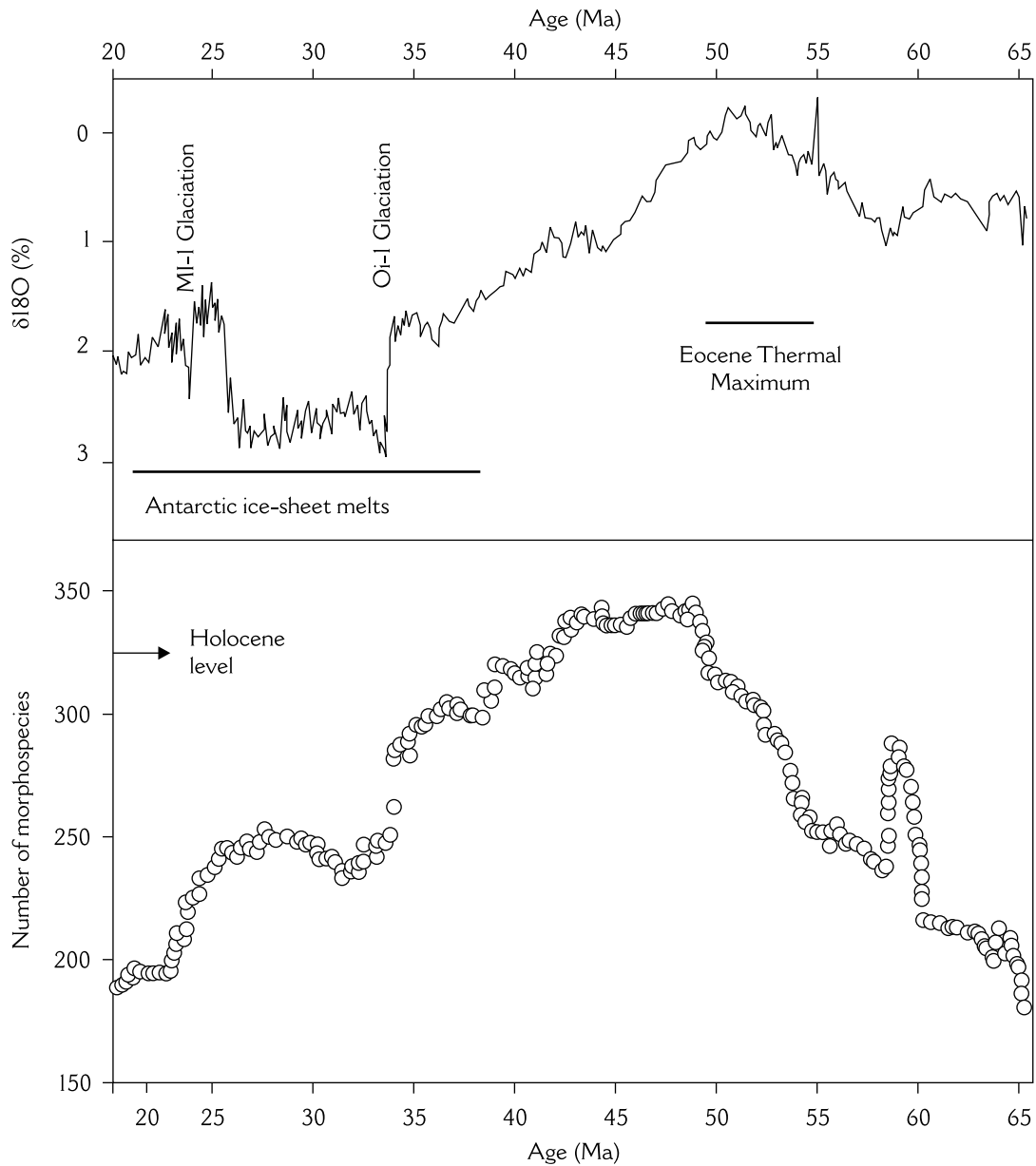


Figure 4 Changes in palynofloral diversity (number of pollen morphospecies) between 65 and 20 Ma (redrawn from Jaramillo *et al.*, 2006). Also indicated are calculated global temperatures obtained from oxygen isotope measurements from marine cores and intervals of thermal maximum and minimum (as evidenced by ice-sheet buildup and glaciation)

at 65–20 Ma (Figure 5) appears to indicate some relationship between intervals of higher diversity in the fossil plant record with intervals of higher temperatures (Jaramillo *et al.*, 2006). This record, containing a compilation of fossil pollen records from sites in central Colombia and western Venezuela, demonstrates higher diversity at times when $\delta^{18}\text{O}$ evidence from ocean records (Zachos *et al.*, 2001) indicates that global temperatures were higher than present. Conversely intervals of lower global temperatures indicate a sharp decline in diversity, in particular from 34 Ma, with the beginning of Southern Hemisphere glaciation and the buildup of ice sheets on the Antarctic continent. However, it is uncertain whether temperature changes affect diversity directly or by changing in the area available for tropical plant growth (Jaramillo *et al.*, 2006). Another question that remains unanswered from this study is whether it is thermal energy or the relationship between water and/or energy fluctuations driving this change. Thus is the decline in diversity from 34 million years ago solely due to temperature change or is it also due to a reduction in water associated with cooling (resulting in less evaporation and hence less precipitation) associated with the continental ice sheets growing at the South Pole?

The relative importance of water and energy on species richness through time has recently been tested using a 320,000-year fossil pollen record from Hungary that dates back to between 3.0 and 2.67 Ma (Willis *et al.*, 2007). In this study, the fossil data set was regressed using ordinary and generalized least squares (GLS) against proxies for palaeoenergy (obtained from orbital calculations of Laskar (Laskar *et al.*, 1993) and palaeohydrological balance (obtained from $\delta^{18}\text{O}$ measurements within the sedimentary sequence) (Figure 6). The results from these regression models indicated that richness was best, in a statistical sense, described by a combined water-energy model where greatest richness occurs at intermediate levels of energy but high levels of water

availability (Figure 6). This study therefore suggested that the influence of energy upon availability of water will also directly affect richness; too much energy will result in the evaporation of water, and conversely too little energy will result in water becoming frozen. At both extremes water will therefore become limiting and this will have a direct impact on richness through various mechanisms including reduced efficiency of metabolic processes, slow rates of nutrient cycling, smaller population sizes, etc (O'Brien, 2006). Such influences have probably had a profound effect on diversity throughout earth's history on tectonic, orbital and millennial timescales.

Further examination of the energy data, however, reveals that it is not just the amount of energy that is important but also the variability of the energy signal. In this sequence there is an additional statistical relationship between the amplitude of the energy signal and richness whereby increased amplitude, be it to hotter or cooler conditions, results in reduced richness (Willis *et al.*, 2007). Thus results from this sequence suggest that it is not only the amount of energy but also the amplitude of the energy changes (variability) that is also important. Examination of the traits of the plant taxa to survive during intervals of wide-amplitude fluctuations suggests that there was a highly deterministic ecological sorting process occurring; those types that survived had traits that included greater tolerance of a cold growing-season and winter temperatures, and to a lesser extent drought.

Preliminary results from these fossil diversity studies are starting to reveal some interesting relationships: (1) the relationship between water-energy dynamics has had a strong influence on diversity through time with evidence from the plant fossil record indicating greatest diversity at high levels of water and intermediate levels of energy; (2) amplitude of energy variation also appears to be a strong determinant of richness with decreased richness correlating with increased climate variability; and (3) certain species

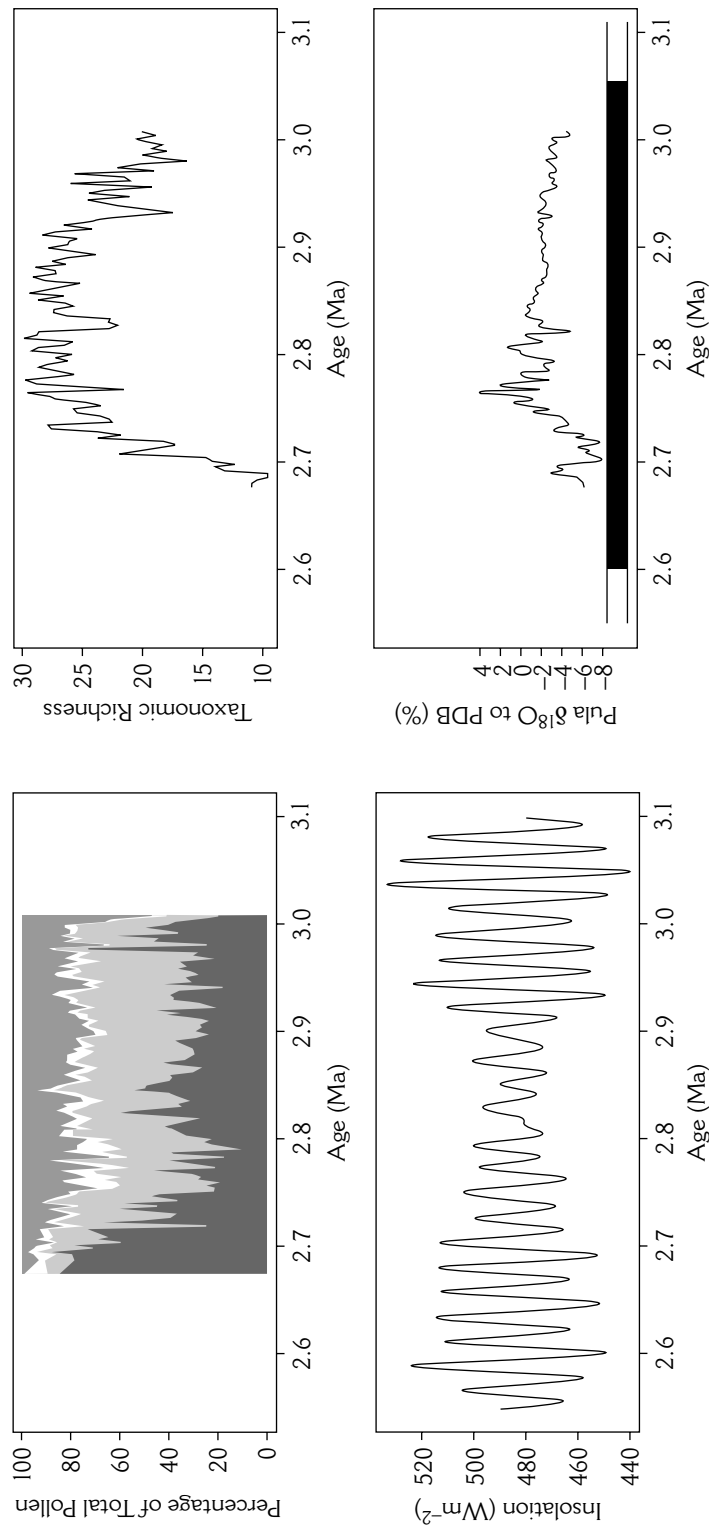


Figure 5 Summary of climatic and biotic components of the explanatory models for plant diversity in Pula Maar, Hungary, at c. 3.0–2.6 Ma (redrawn from Willis *et al.*, 2007): (a) the fraction of total pollen for boreal (black), cool-temperate (light grey), herbaceous (white) and warm-temperate (dark grey) taxa; (b) the estimated taxonomic richness; (c) Energy input estimated from June insolation (Wm^{-2}) based on the orbital calculations of Laskar *et al.* (1993) at 47°N for the period between c. 3.0 and 2.6 Ma (Willis, 1999a; 1999b); (d) Water availability estimated using $\delta^{18}O$ (d – bottom line)

appear to be more susceptible to climatic variability according to their ecological traits.

The fact that greater variability in energy flux appears to have resulted in an increased extinction rate (local and, in some instances, global) is something that has not previously been determined using spatial data sets. It is probable that this effect has occurred throughout earth's history and may well be why, for example, so few originations are apparent in the Quaternary fossil record and the predominant mode is one of reduced diversity (Willis and Niklas, 2004) – because this has been an interval of increasingly wide amplitude fluctuations in energy combined with reduced water availability, especially in mid- to high latitudes. This result also is very much in line with the recent work by Weir and Schuller (2007) which concluded that it is decreased extinction rates that presently lead to patterns of higher diversity in some regions. Such findings have important implications for predicting richness at times of increasing climate variability.

VI Climate change, community reorganization and morphological responses evident in mammalian fossil records

While palaeoenvironmental records have long yielded evidence of the dynamic nature of animal and plant distributions in response to climate change, more recent work is providing important insights into the evolutionary capability of organisms to respond to this and other environmental perturbations through morphological changes. Palaeoecological studies on mammals have documented the entire gamut of responses possible, including tolerance, local extirpation and range shifts, as well as adaptive changes in genetics and/or morphology (eg, Graham, 1986; Dayan *et al.*, 1991; Smith *et al.*, 1995; FAUNMAP Working Group, 1996; Hadly *et al.*, 1998; Smith and Betancourt, 1998; 2003; 2006; Grayson, 2000; Millien and Jaeger, 2001; Barnosky *et al.*, 2003; Lyons, 2003; 2005; Chan *et al.*, 2005; MacPhee *et al.*, 2005;

Blois *et al.*, 2007). Not only are the fossil and subfossil records for the late Quaternary particularly abundant, especially for mammals, but it was also a period of considerable (and well-documented) fluctuations in climate. Fine-scale palaeoclimate reconstructions generated using pollen, tree-ring chronologies, ice cores and other indicators, for example, have resulted in a new appreciation of how rapidly and frequently shifts in the earth climate system occurred (eg, Allen and Anderson, 1993; Dansgaard *et al.*, 1993; Bond and Lotti, 1995; Dahl-Jensen *et al.*, 1998; Bond *et al.*, 1997; Alley, 2000). A sampling of recent palaeoecological studies examining mammalian distribution, abundance and morphology over the late Quaternary are reviewed here. These vary from work on individual populations and/or single species to those studies addressing the 'stability' and resistance of entire communities to environmental changes over time. The common thread is the unique insights into ecological and evolutionary responses possible with a long-term historical perspective.

Similar to fossil pollen-based studies of Quaternary plant communities, one critical issue in mammalian studies has been determining the extent to which species assemblages are cohesive or stable, rather than dynamic with associations changing repeatedly over time (eg, Graham, 1986; Graham and Mead, 1987; Graham and Grimm, 1990). Clearly, this is fundamental to understanding the structure and function of modern communities and their 'resilience' to climate change. The creation of the FAUNMAP database has been central to the ability to analyse mammalian community structure over the late Quaternary (Graham *et al.*, 1996). FAUNMAP (<http://www.museum.state.il.us/research/faunmap/>) is a relational database containing detailed information on species composition, geological age and stratigraphy for almost 3000 fossil localities across the United States spanning the last 40,000 years; it is integrated with a geographical information system and publicly

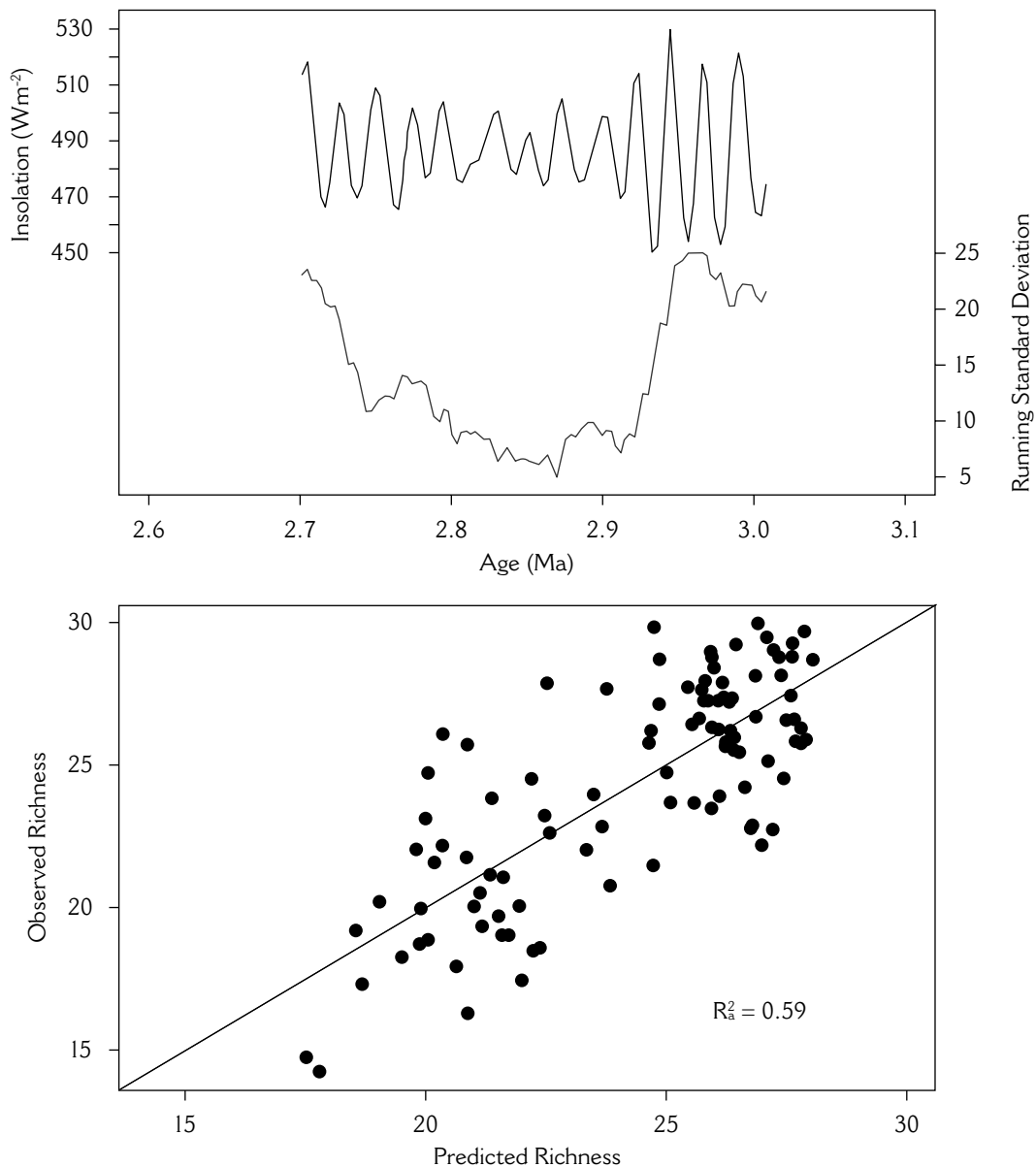


Figure 6 Taxonomic richness recorded in the pollen record of Pula core regressed against insolation data (a proxy for energy), Pula $\delta^{18}\text{O}$ (a proxy for water availability) and the variability of the amplitude in insolation (a – top line) (redrawn from Willis *et al.*, 2007). Variance of the energy signal is expressed through its 32 ky (11 data points) running standard-deviation (a – bottom line). Results indicated that the magnitude of the amplitude in the energy signal provides additional explanatory power when combined with the water-energy model (= 0.59) to produce ordinary least squares and generalized least squares models with the lowest Akaike information criterion, as illustrated in (b) by the scatterplot of measured and predicted richness and (c) temporal dynamics of observed (c – top line) and predicted (c – bottom line) richness

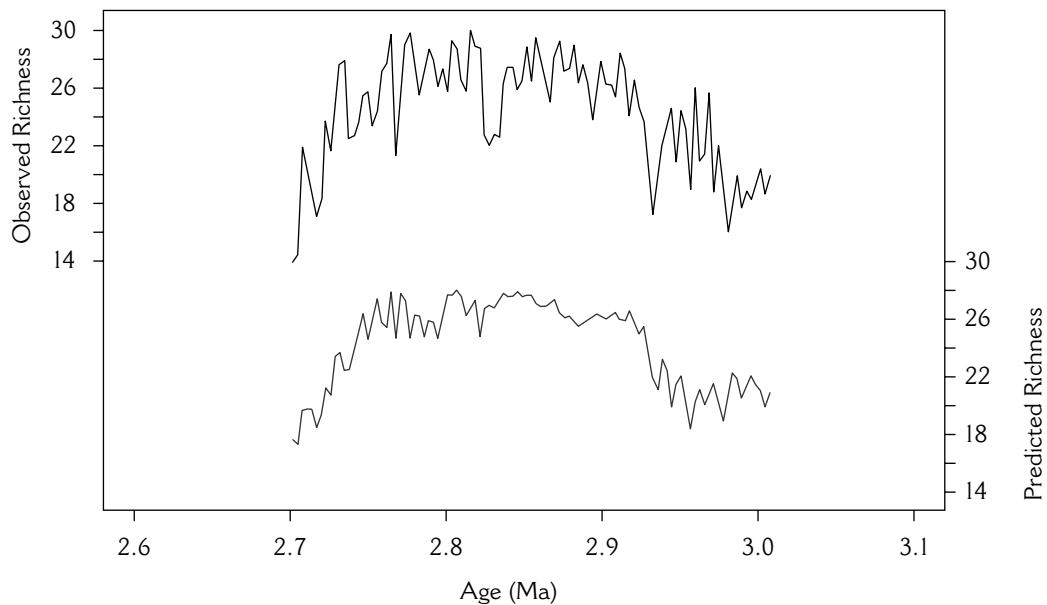


Figure 6 (continued)

accessible. This resolution allows the examination of changes in the distribution of individual species as well as entire assemblages.

Initial qualitative analysis of the FAUNMAP data suggested that the geographical ranges of individual mammal species shifted at different times and in different ways in response to the changing climatic regimes of the late Quaternary, and further, that the emergence of modern communities was fairly recent (Graham *et al.*, 1996). The common presence of non-analogue communities (assemblages of animals that do not occur together today) throughout the Pleistocene led the authors to conclude that ‘mammal communities are continually, and unpredictably, emergent’ (Graham *et al.*, 1996: 1605). Thus, models aiming to predict responses to anthropogenic warming would need to target individual species and their requirements, rather than biotic provinces; a rather daunting task. The FAUNMAP data was reanalysed by Lyons (2003; 2005) using a quantitative approach. In a series of elegant studies, she used occurrence data of mammalian species represented in the FAUNMAP database

to construct distribution maps represented by convex polygons for four discrete time periods over the late Quaternary. The extent to which the species range changed between time intervals was characterized by comparison of the median position (i.e., the centroid) of the range, the overall estimated size and the direction of centroid shift, if any. She found that main species exhibited very small range shifts from one time transition to another. The average centroid shift was between 1200 and 1400 km; this value did not vary substantially temporally. Directionality was most striking for the Glacial-Holocene transition, with ranges tending to shift south and southeast (Lyons, 2003). The overall pattern of community similarity over time was neither cohesive nor completely dynamic. Although non-analogue communities were found in each time transition, simulation analyses suggested that many communities were significantly more similar through time than expected by chance (Lyons, 2005). This would seem to suggest that many mammals shared a common response to altering climatic regimes.

Whether such similarities stemmed from co-evolved and obligate biotic interactions, however, or because species shared common environmental requirements was unclear (Lyons, 2005). Clearly, the degree to which generalities can be made about species distributional responses to climatic changes still remains to be resolved.

It has been argued that morphological shifts are the simplest way for mammals to respond to environmental change and, further, that such changes might well precede detectable shifts in species abundance or distribution (Barnosky *et al.*, 2003). A number of palaeoecological studies have documented the ability of mammals to respond to temperature by morphological changes in size or shape. Using a highly resolved palaeorecord unique to North America, for example, Smith and her colleagues (Smith *et al.*, 1995; Smith and Betancourt, 1998; 2003; 2006) examine the adaptive response of *Neotoma* (woodrats) to late-Quaternary climate shifts across their range. These studies employ ancient woodrat middens – fossilized plant fragments, fecal pellets and other materials gathered by woodrats and held together in an indurated conglomerate of evaporated urine. Middens are ubiquitous at arid sites across the western United States (Betancourt *et al.*, 1990). An online database of midden records from the United States can be used to access this rich archive (<http://esp.cr.usgs.gov/data/midden/>). The most finely resolved sites contain dozens of discrete deposits spanning 20,000 years or more; each of which yields estimates of population body mass, genetics, diet and deposition date. Thus, the morphological and genetic responses of populations to climate fluctuations over thousands of years can be characterized. In general, woodrats adapted to late-Quaternary climate change by morphological shifts in body size (Smith *et al.*, 1995; Smith and Betancourt, 1998; 2003; 2006). The response follows the predictions of Bergmann's rule; woodrats were larger during cold intervals and smaller

during warmer episodes. Patterns were remarkably concordant across the entire distributional range, probably reflecting common environmental fluctuations over the late Pleistocene (Smith and Betancourt, 2006). Responses were more complicated at range boundaries where animals approach the limit of their physiological and ecological thermal tolerances (Smith and Betancourt, 2003). At range boundaries, high-elevation populations demonstrate a Bergmann's rule response to climate shifts, while low-elevation populations display a variety of responses depending on the location and severity of the environmental shifts. Such robust patterns of body size and temperature were also seen with contemporary species (Smith *et al.*, 1995; Smith and Betancourt, 1998; 2003; 2006). Laboratory and field studies with modern animals suggest physiological constraints may be the underlying mechanism; maximum, minimum and lethal environmental temperatures all scale inversely with body mass (Smith *et al.*, 1995).

In recent work, Smith *et al.* (2008) investigated the influence of late-Quaternary climate change on two different rodent species along steep height and environmental gradients in Death Valley, California. Today, Death Valley is the hottest and driest area in the Western Hemisphere with temperatures of 57°C recorded. During the late Quaternary, however, pluvial Lake Manly covered much of the valley and contributed to a climate as much as 6–10°C cooler (van Devender and Spaulding, 1979; Thompson *et al.*, 1999; Mensing, 2001; Koehler *et al.*, 2005). By analysing a series of 74 'palaeomiddens' recovered from a 1300 m height transect through the Grapevine Mountains, Smith *et al.* (2008) documented the changing distribution of these species over the last 24,000 years. They were able to characterize the temperature thresholds leading to adaptation versus displacement along the height gradient and, moreover, document the eventual extirpation of one of the species. Although previously unknown

from the eastern side of Death Valley, *N. cinerea* was ubiquitous in this region during the Pleistocene, extending down to 800 m elevation. Moreover, the presence of this species was apparently also tied into the downward displacement of juniper by almost 1000 m.

One particular benefit to working on relations in the late Quaternary is that the species of interest are extant. The integration of a historical perspective with studies on contemporary populations or communities is a powerful approach to disentangling causal mechanisms. Insight into the underlying mechanisms behind woodrat sensitivity to climate, for example, was possible because of lab and field work demonstrating the tight relationship between temperature and body size in contemporary animals (eg, Lee, 1963; Brown, 1968; Brown and Lee, 1969; Smith *et al.*, 1995). But temperature is not always the climatic variable of importance. Recently, Blois *et al.* (2007) conducted a detailed examination of the abiotic and biotic factors underlying geographical patterns of body size variation in California ground squirrels (*Spermophilus beecheyi*). They found that the characteristic body size of populations was best explained when patterns of precipitation across the spatial gradient were incorporated into regression models. Comparison of these 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.*, 2007). Similarly, in a classic 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 species of carnivore over the late Quaternary. By integrating geographical 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, not temperature or precipitation shifts, was responsible for producing the patterns of carnivore body-size changes observed. The

importance of biotic interactions on size patterns, especially combined with climate, has been found elsewhere as well (eg, Millien-Parra and Loreau, 2000; Millien, 2004; Millien and Damuth, 2004).

Because of the nature of fossil materials, many palaeoecological studies of mammals are community-based. Most fossils tend to be recovered from excavations, which often entails the removal and sorting of large quantities of materials. Lamar Cave, a particularly rich fossil site from northern Yellowstone National Park in Montana, for example, has yielded an exceptional record of small mammal populations over the last 3200 years. To date, more than 10,500 mammal specimens have been recovered, allowing examination of morphology, genetics, abundance and community composition over the last 3000 years (eg, Hadly, 1996; 1999; Hadly *et al.*, 1998). Some of the more common fossils found are those of pocket gophers (*Thomomys talpoides*), which demonstrate both morphological and ecological sensitivity to Holocene climate shifts (Hadly, 1996; 1999). Not only do gopher size-related craniodental characters vary in size, decreasing during the warmer conditions of the MCA (AD ~900–1300), but there are also significant changes in abundance related to shifts in the vegetative community. Other species in the palaeo-community also demonstrated predictable shifts in abundance that appeared to be related to the absence or presence of preferred habitat types (Hadly, 1996; 1999). For these species, shifts in vegetation, rather than climate itself, appeared to be the main driver behind observed changes. Interestingly, little genetic variation is found in gophers through time; both ancient specimens and modern samples share mitochondrial cytochrome b sequences absent from adjacent localities, suggesting not only that the population was isolated for the entire period, but also that there was little genetic response to late-Holocene climatic fluctuations (Hadly *et al.*, 1998). In contrast, body size changed predictably in response to climatic change.

Interestingly, recent work has demonstrated that the relationship between mammalian community structure or morphology and palaeoclimate can be examined from a completely different perspective. Characteristics of the assemblages themselves can be used to infer palaeoclimate. This approach has been used by Montuire (1999) to interpret the pattern of climatic and environmental change over the Plio-Pleistocene of Europe, by Damuth *et al.* (2002) to develop predictive equations relating dental morphology of mammalian communities to precipitation and temperature patterns, and over deeper time intervals by Fortelius *et al.* (2002; 2006) and others (eg, Montuire and Marcolin, 2002; Legendre *et al.*, 2005; Montuire *et al.*, 2006). The use of dental characteristics is particularly informative. Fortelius *et al.* (2002) used the relationship between the type of teeth (ie, level of hypsodonty) of herbivorous mammals and vegetation to reconstruct palaeogradients of aridity and temperature across the Eurasian continent over the last 20 million years. Such research holds much promise for reconstructing past climates.

VII Climate change and the genetic basis of Quaternary evolution from the analysis of DNA from fossil plant material

There is a well-developed pollen-based record of plant dispersal on the northern continents at the end of the last glaciation (Davis, 1976; Huntley and Birks, 1983). Ferris *et al.* (1995) and Petit *et al.* (1997) have related these fossil-based distributions to modern patterns of DNA variation, providing important and significant linkage between the fossil temporal patterns and modern spatial patterns. However, although fossil patterns display past distributions simply and effectively, they cannot display ancestries of populations. Hypotheses about the ancestry of populations and how they are affected by Quaternary-scale climate change (eg, Cwynar and MacDonald, 1987; Bennett *et al.*, 1991)

remain untested. New molecular approaches to Quaternary palaeobiogeography offer the potential to address these questions.

Modern taxonomy relies heavily on the DNA similarities and differences between individuals, populations and species. In the last 10 years, ancient DNA (aDNA) has been successfully extracted from fossil organisms and results from specimens of late-Quaternary remains (up to 100 ka – 100,000 years ago) have provided insights on evolutionary processes, particularly in animal species (eg, Krings *et al.*, 1997; Brown, 1999; Leonard *et al.*, 2000; Cooper *et al.*, 2001; Endicott *et al.*, 2003; Hadly *et al.*, 2004). Initial aDNA reports suggested that the time period open to investigation could be vast (Golenberg *et al.*, 1990; Soltis *et al.*, 1992). However, theoretical and empirical considerations have since showed that aDNA is highly affected by hydrolytic and oxidative damage (Paabo and Wilson, 1991; Lindahl, 1993). As a consequence, the retrieval of DNA sequences older than about 100 ka is expected to be difficult to achieve, and the criteria that need to be met in order to eliminate the possibility of contamination are rigorous (Hebsgaard *et al.*, 2005; Willerslev and Cooper, 2005). Methodological difficulties, problems with contamination and the rarity of suitable fossilized samples have often prevented a broader utility for aDNA studies at the population level. This is particularly so with plants, where well-preserved fossilized hard tissues, such as wood, can be difficult to obtain in sufficient number, over large enough geographical areas. Nevertheless, in the last two decades, aDNA has been successfully extracted from plant material too (Gugerli *et al.*, 2005), including now subfossil wood (Liepelt *et al.*, 2006; Deguilloux *et al.*, 2006), but so far with little direct impact on ancestry reconstruction.

A number of recent investigations have extracted DNA from bulk sediments of permafrost (Willerslev *et al.*, 2003; Lydolph *et al.*, 2005) or lakes (Coolen *et al.*, 2004). Since the organism that produced the DNA is not

available, the technique is most useful in identifying and listing taxa that may have been present. The alternative approach, extracting DNA from identified fossils, has been more useful in reconstructing past lineages (eg, Leonard *et al.*, 2000). Pollen contains haploid DNA and is the means of its dispersal to the haploid DNA of the ovules. It consists of two or three haploid cells (large vegetative cells enclosing one single or two generative cells), including several plastids and mitochondria. Organellar DNA (plastids and mitochondria) is therefore present in pollen. Pollen from species with paternal inheritance of plastid DNA, such as at least six of the seven families of conifers (Mogensen, 1996), is rich in plastid DNA at maturation, and the existence of these multiple copies makes this source of DNA the best prospect for aDNA studies in pollen. Nuclear DNA, in contrast, is present only as a single copy (and is also subject to recombination, which complicates the analysis in phylogeographical terms). Plant mitochondrial DNA evolves too slowly (Soranzo *et al.*, 2000). Plastid DNA has been shown to be ideal for phylogeographical reconstruction (Ennos *et al.*, 1999).

Preserved pollen in sediments is one of the most numerous Quaternary fossil remains routinely investigated. Concentrations in organic lake sediments can exceed 105 grains cm^{-3} (eg, Maher, 1972), typically dominated by pollen from wind-pollinated plants, including conifers. As a source of aDNA, pollen suffers from the disadvantage that from each grain there is only one chance for extraction of each DNA type (be it nuclear, plastid or mitochondrial), in contrast to multicellular objects (such as bone, tissue, wood) where there are multiple opportunities for extraction of a given sequence from the same genome. Replicability comes from the ready access to very large numbers of grains, giving the possibility of a statistical population of genotypes, rather than heavy dependence of successful extraction from a few (or even one) genotypes.

Pollen retrieved from Holocene lake sediments (up to 10,000 cal yr BP) offers several

advantages for aDNA studies. Depositional conditions are fast and this reduces physical damage of the grains. Burial is usually rapid and this contributes to reduce the exposure of the grains to biotic degradation, to protect the environment of the fossil and to prevent percolation through the sediment sequence. Pollen grains are found in high concentrations ($>100,000$ grains cm^{-3}) and are usually very well preserved. Because of their relatively young age, they are less affected by diagenesis and therefore more likely to preserve DNA molecules.

Another advantage conferred by the relatively young age of this material is that, by using appropriate molecular markers, lineages of Holocene specimens can be traced directly to living specimens. Thus extant sequences can easily be compared with the ancient ones and links can be made with modern populations. Finally, the fine degree of chronological precision that can be obtained in the Holocene enables the establishment of a detailed timescale and the application of dating methods, such as radiocarbon, can in some cases provide a high degree of accuracy requiring small amounts of material. Suyama *et al.* (1996) succeeded in amplifying a short region of chloroplast DNA from four pollen grains of *Abies* older than 100 ka collected from a Quaternary peat at Kurota Lowland, Fukui, Japan. The same technique was used later to isolate DNA from Holocene pollen of *Pinus sylvestris* retrieved from lake sediment in central Sweden, and showed that chloroplast DNA is recoverable from *Pinus sylvestris* pollen grains that are 100 years old and 10,000 years old (Parducci *et al.*, 2005). The method is also been successfully applied to the analysis of chloroplast variation in 45 ka pollen grains from the angiosperm tree *Fagus orientalis* (Paffetti *et al.*, 2007), which had been expected to show only maternal inheritance of plastid DNA.

As pollen is probably the most widely available and numerous Holocene fossil, continued development of the extraction of DNA from fossil material will bring on stream a technique that will contribute powerfully to

questions of plant movement in space and time by bringing the taxonomic resolution down from species or generic level to population or species level. Improving understanding of how plants respond to climate change at millennial scales at a taxonomic level appropriate for comparisons with plant ecology will radically change the relationship between palaeoecology on the one hand and plant population ecology/genetics on the other. An effective synthesis of the two has hitherto been hampered by lack of contact points in terms of taxonomy and temporal or spatial resolution, but aDNA work should bridge that (Bennett and Parducci, 2006).

VIII Conclusions

Understanding climate change and its impacts on the biosphere is one of the defining challenges of twenty-first century biogeography and conservation. The preceding sections have presented a broad overview of some of the exciting fronts along which Quaternary and Cenozoic palaeobiogeography is advancing. It is clear that the discipline has developed well beyond an exercise in natural history that is concerned simply with chronicling past environments from a single site or region. Research in Cenozoic palaeobiogeography is now integrated within broader efforts to test biological and climatological hypotheses, to develop new models and to advance ecological, evolutionary and earth systems theory. Palaeobiogeographical studies can not only document how species distributions reacted to past environmental change, but also have the potential of documenting how individual species reacted phenotypically and genotypically to such changes. Given the pressing challenges of ongoing habitat fragmentation and climate warming, the application of the palaeostudies for conservation purposes will undoubtedly increase.

The preceding sections echo some common themes that help to explain why Quaternary palaeobiogeography is so successful and exciting at this time. Three

common factors that drive the current dynamism can be identified as follows. First, new tools for resolving past species distributions and environments continue to be developed while traditional tools are become increasingly refined. The use of biomarkers in lake sediments to reconstruct limnic and terrestrial species distributions and the extraction of DNA to from fossil pollen in order to conduct population genetics research are two of the most striking examples of these new tools. Second, the number of palaeorecords has increased and many of these have been collated into global data sets that are easily available online. These data networks allow a broad range of researchers to ask questions at the synoptic scale and rapidly compare past species distributions to the contemporary climatic conditions. Third, the research and training of Quaternary palaeobiogeographers reflects an increasing degree of integration with evolutionary biology and earth systems science. Fundamental questions arising from these disciplines are being recognized as tractable through palaeobiogeographical research. In addition, observations and hypotheses from palaeobiogeographical research are catching the attention of molecular geneticists or climate modellers and forming part of their research programmes. This developing integration between the life and earth sciences is at the heart of earth systems science and is the way of the future. An integrated earth systems science approach is particularly critical considering the challenges being faced due to global warming. Understanding past environmental changes and their impacts through Quaternary palaeobiogeography, and extension of these techniques to the earlier Cenozoic will be a key component of that science.

What important substantive results arise from the reviews presented here, particularly in relationship to anticipated future climate change? A pervasive message is that the climate has been dynamic at many different timescales and that biota have responded

in a similarly dynamic fashion. The climatic variations have included not only long-term millennial changes in mean conditions, but also much shorter-term shifts, and changes in variability. The assumption of stationarity is a short-term illusion in terms of both climate and the impacted biota. The shifts in climate have also impacted disturbance regimes such as fire and this has had a sharp impact on populations and landscapes. Finally, some shifts in climate may have been gradual, but events such as the YDE or the MDA and LIA were much more rapid. Responses to climate changes have included changes in geographical distributions, shifts in community composition and extinction. Species which are extant today have in the past been organized into communities that have no modern counterparts. Regional biodiversity has seen marked changes in response to shifts in climate. In addition to these ecological responses, which are expected in the case of large-scale habitat changes and climate warming, there is also evidence that species have responded with genotypic and phenotypic shifts in the face of Quaternary climatic change. Such evolutionary responses should also be anticipated in the future. Considering the future shifts in climate that are projected due to greenhouse warming, it is clear that Quaternary palaeobiogeography offers increasingly well-resolved evidence on both the sensitivity and the potential resilience of the biosphere to such change.

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