Long-Term Ecological Records and Their Relevance to Climate Change Predictions for a Warmer World

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Abstract

This review focuses on biotic responses during intervals of time in the fossil record when the magnitude and rate of climate change exceeded or were comparable with those predicted to occur in the next century (Solomon et al. 2007). These include biotic responses during: (*a*) the Paleo-Eocene Thermal Maximum and early Eocene Climatic Optimum, (*b*) the mid-Pliocene warm interval, (*c*) the Eemian, and (*d*) the most recent glacial-interglacial transition into the Holocene. We argue that although the mechanisms responsible for these past changes in climate were different (i.e., natural processes rather than anthropogenic), the rate and magnitude of climate change were often similar to those predicted for the next century and therefore highly relevant to understanding future biotic responses. In all intervals we examine the fossil evidence for the three most commonly predicted future biotic scenarios, namely, extirpation, migration (in the form of a permanent range shift), or adaptation. Focusing predominantly on the terrestrial plant fossil record, we find little evidence for extirpation during warmer intervals; rather, range shifts, community turnover, adaptation, and sometimes an increase in diversity are observed.

1. INTRODUCTION

What does a warmer world mean for global biodiversity? Atmospheric CO_2 likely will increase to close to 1,000 ppmv over this century (Solomon et al. 2007), and global temperatures are widely anticipated to increase by 2–4°C and possibly beyond (Meinshausen et al. 2009). Sea levels will rise ~1 m $\pm$ 0.5 m (Nicholls & Cazenave 2010). The subtropics will become drier, whereas other regions, such as portions of the tropics and higher latitudes, will become wetter (Solomon et al. 2007). Increases in climate variability and frequency of extreme weather events are also predicted. The spatial variation in warming will be pronounced; areas such as the Arctic will experience the highest magnitudes and most rapid rates of warming, with annual temperatures increasing by 6 to 7°C, whereas portions of the North Atlantic and southern oceans may warm only by 0.5 to 1.0°C (Solomon et al. 2007). In general, land areas likely will experience increases in annual temperature of 2 to 4.5°C by the end of the century (**Figure 1**).

Aside from simply warmer temperatures, perhaps a quarter of the Earth's surface will experience climatic conditions that have no close analog in the present climate (Williams et al. 2007). The high amounts of CO_2 will affect rates of photosynthesis and water-use efficiency for plants, and this coupled with the nonanalog climate means that species' realized niche conditions relative to temperature and water may be altered (MacDonald 2010). Furthermore, the rates of the temperature and climate changes will be rapid according to some models, for example, a predicted rise of 0.41°C decade^{-1} [Intergovernmental Panel on Climate Change (IPCC) A2 scenario] in tropical regions (Solomon et al. 2007). Notably, annual temperature trends from 1951 to 2009 already show increases over the continents as high as 2°C in the high northern latitudes and 0.5 to 1°C over large continental areas at the lower latitudes (**Figure 1**). This is equivalent to an ~0.34°C decade^{-1} to 0.09°C decade^{-1} rate of change already. Many of the regions subject to the greatest
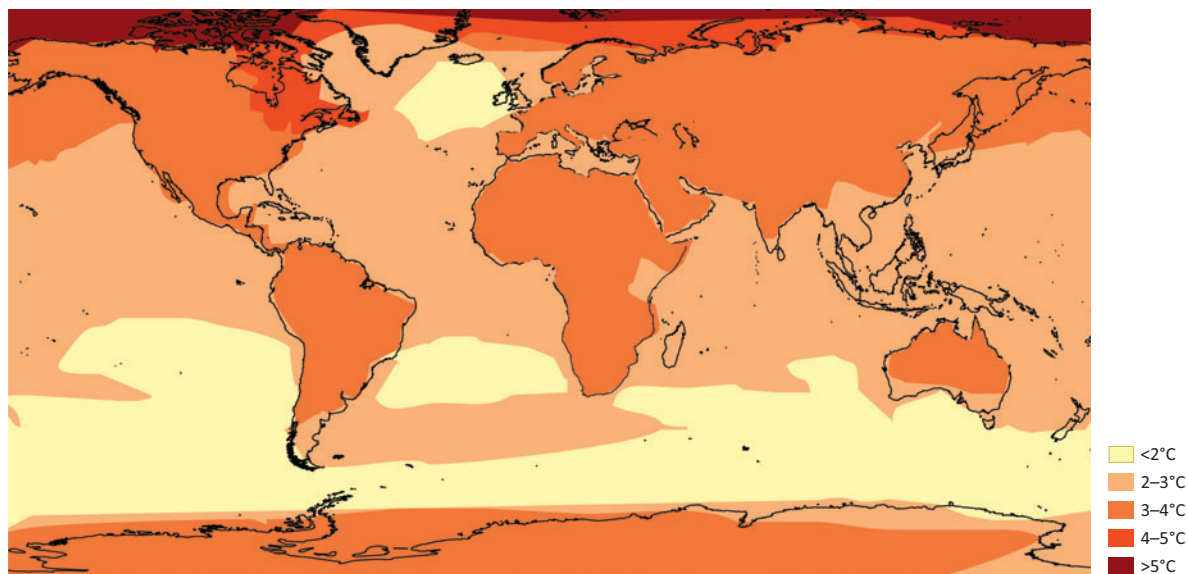

Figure 1

Projected surface temperature increases for the late twenty-first century (2090–2099) based on the multi-Atmosphere-Ocean General Circulation Model average projection for the A1B SRES scenario. Temperatures are relative to the period 1980–1999 (Solomon et al. 2007, figure SPM 6).

anticipated increases in temperature have relatively low biodiversity today, such as the Arctic or the Sahara and Namibian deserts; however, of the world's biodiversity hot spots, the Amazon is expected to experience particularly pronounced warming.

Anticipated impacts of the predicted climate changes on the Earth's biota can be broadly classified under three possible scenarios: extirpation, migration (in the form of a permanent range shift), or adaptation (Aitken et al. 2008). To date, key research efforts have focused on the first two scenarios, mainly through the assessment of biotic responses to climate change via development of a suite of predictive species distribution models (e.g., Guisan & Thuiller 2005). These bioclimatic envelope models predict current and future range shifts and estimate the distances and rates of movement required for species to track the change in climate and move into suitable new climate space (e.g., Thuiller et al. 2008).

Extirpation results from loss of suitable climate space, slow rates of movement in response to climate change, and other proposed mechanisms including increased variability of climate and frequency of extreme events, altered ecosystem interactions, and a climate-related increase in vectors carrying disease (e.g., Millar et al. 2007). Model output has provided some depressing predictions for species loss by 2050. One of the most-cited studies is that of Thomas et al. (2004), which predicts that, on the basis of mid-range climatic warming scenarios for 2050, up to 37% of plant species globally will be committed to extinction owing to lack of suitable climate space. Another well-cited scenario is the prediction from a general dynamic vegetation model run for the tropical forest biome (Huntingford et al. 2008) that a loss of up to 80% of the tropical forest biome will occur in the next 50–80 years; savannah will replace the majority of the tropical forest. Extinction predictions associated with these models are focused primarily on the potential reduction in population size (sometimes down to nothing).

On the key question of whether biota can move fast enough to track the climate change, modeling output and data from fossil and molecular records paint a bleak picture (Loarie et al. 2009). In Malcolm et al. (2002), which examined output from 14 general circulation models (GCMs) and global vegetation models (GVMs), the results indicated that for many plant species, rates of up to 1,000 m year^{-1} or more are necessary to track suitable habitat under predicted climate change. A more recent analysis shows that even under conservative IPCC estimates of twenty-first century greenhouse gas emissions and warming, species in large areas of the tropics will need to migrate 500 km or more to stay within their current climatic space by the end of the century (Williams et al. 2007). Other recent scenarios suggest that even species that occupy large areas of the higher latitudes will face similar migrational challenges (Loarie et al. 2009). Mathematical models of plant migration suggest that rates may be more typically on the order of <100 to <10 m year^{-1} (Clark et al. 2001, Higgins et al. 2003, Svenning & Skov 2007). Model predictions for the migration rates of five tree species in the eastern United States, for example, indicate very low probabilities of dispersal of more than 10–12 km by 2050 (Iverson et al. 2004).

In comparison with extirpation and migration, biotic adaptation to climate change has been considered much less frequently. Sometimes referred to as evolutionary resilience, it is the ability of populations to persist in their current location and to undergo evolutionary adaptation in response to changing environmental conditions (Sgro et al. 2010). This approach recognizes that ongoing change is the norm in nature and one of the dynamic processes that generates and maintains biodiversity patterns and processes (MacDonald et al. 2008a, Willis et al. 2009).

The ability of an organism to adapt to a new environment results from adaptive genetic diversity (Sgro et al. 2010), that is, variation in genes that enables an adaptive response. This adaptive response may be manifest as a behavioral trait, a morphological trait, and/or plasticity in physiological tolerances to the climate change. Some elegant examples of adaptive genetic diversity

to recent climate change are emerging in the literature. For example, in a 47-year study of the great tit (*Parsus major*) in the United Kingdom, Charmantier et al. (2008) demonstrated that individual adjustment of behavior in response to the environment has enabled the population to track a rapidly changing environment closely and that in this population, phenotypic plasticity can play a central role in tracking climate change. The ability of many trees to persist well outside of their realized ecological niches (under reduced competition) is another example that is apparent in botanical gardens throughout the world (Aitken et al. 2008).

One of the key limitations in detecting whether an organism, a population, a community, or even a biome can survive climate change is lack of suitable empirical data sets. Few data sets span a sufficient length of time and a climate change interval similar in magnitude and/or rate to those predicted over the next century. For organisms with longer generation times, for example trees and large mammals, this is particularly problematic because the usual transplantation methods (often termed "garden experiments"), in which the organism is moved to a different climatic area and its responses assessed (through genotypic and/or phenotypic methods), will not yield results for decades.

Although long used in plant migration studies, paleoecological records have, as yet, been underutilized in analysis of adaptation and biodiversity conservation in the face of climate change. In several important intervals over the past 57 Myr, global or superregional temperatures and in some cases CO_2 levels have been comparable with or higher than those predicted for the next 100 years or so (Royer 2008, Zachos et al. 2008). The rate of some of these climate changes has also been similarly rapid as those predicted for the future (Steffensen et al. 2008). Paleoclimate records in conjunction with paleoecological records therefore provide an important framework in which to assess the resilience of biota to a warmer world (Willis & Bhagwat 2009, Willis et al. 2010b). Although determination of the genotypic variation enabling adaptation is, as yet, difficult from fossil records, these longer-term records can provide an important framework to assess phenotypic responses at the population, community, and even biome scale.

The aim of this review, therefore, is to examine several previous intervals of Earth's recent history in which the climatic conditions were as warm, or warmer, than those predicted for the next 100 years, and for each interval in time, to examine the evidence for biotic response and impacts on biodiversity. The intervals of time on which we focus include the Paleocene-Eocene Thermal Maximum, the Eocene climatic optimum, the mid-Pliocene warm interval, the Eemian interglacial, and the Holocene. The key objective is to determine predominant responses (extinction, migration, or adaptation) during these intervals of warmer climate for specific case studies and/or regions and to compare these responses with those predicted from the modeling and other studies described above. Often the focus is on plants, as they are widely represented in the fossil record and provide both food and in many cases the habitat upon which other components of the biota are dependent.

2. PALEOCENE-ECOCENE THERMAL MAXIMUM AND EOCENE CLIMATIC OPTIMUM (56–51 MYR)

The first interval of time to examine is between 56 and 51 Myr. This is a particularly interesting time because it is estimated to have been one of the warmest intervals in Earth's history and to have had the lowest equator-to-pole temperature gradient of the past 55 Myr (Blois & Hadly 2009, Moran et al. 2006). Evidence from various paleoclimatic proxies indicate that at the beginning of this interval, global temperatures rose by ∼5°C in 10,000 years (Zachos et al. 2001) with average values in northern tropics during the Paleocene-Eocene Thermal Maximum (PETM) (56.3 Mya) estimated to have been ∼31–34°C. By the Eocene Climatic Optimum (53–51 Mya), tropical

temperatures were between 5 and 10°C warmer than present (Zachos et al. 2008). Paleoclimatic estimates derived from paleosols, phytoplankton, and stomatal density indices also indicate that atmospheric CO_2 was considerably higher, with values exceeding 1,200 ppmv (compared with the present value of ∼400 ppmv). An interesting biological indicator of the warmer temperatures during this time is the fossil remains of a giant boid snake found in northeastern Colombia and dated to a slightly earlier age of 58 Myr (Head et al. 2009). This fossil snake has an estimated body length of 13 m and a mass of 1,135 kg, which make it the largest known snake. The maximum size of a poikilothermic animal at a given temperature is limited by its metabolic rate, and a snake of this size would require a minimum mean annual temperature of 30–34°C to survive (Head et al. 2009).

The higher temperatures predicted between 56 and 51 Mya are comparable with those predicted to occur in the next century as a result of anthropogenically induced climate change. These predictions have led to forecasts of biotic loss including widespread extinctions and large-scale die-back of the tropical rainforest biome (Cox et al. 2004, Huntingford et al. 2008; but see Zelazowski et al. 2011). What was the response of biota in the past to these higher temperatures: extirpation, migration, or adaptation?

Several good fossil records are available to examine the biotic responses to climate change; these range from high-resolution palynological records in the Neotropics (Jaramillo et al. 2006, 2010) (**Figure 2**) to macrofossil and palynological records in North America (Harrington & Jaramillo 2007, Wing et al. 2005) and macrofossil assemblages in the Arctic (Taggart & Cross 2009) and Antarctica (Morley 2007). From these records, evidence for all three responses is apparent, but interestingly, the most pronounced is one of persistence; in some regions an increase in biodiversity occurred owing to the appearance of many new species, mostly angiosperms (Jaramillo et al. 2010). Each response is discussed in turn.

Despite evidence for large-scale biotic turnover, little evidence suggests large-scale global plant extinction during this interval of enhanced warmth. Probably the best records to demonstrate this are three Neotropical pollen diagrams from Colombia and Venezuela that contain the finest scale of taxonomic and temporal resolution across the PETM warming (Jaramillo et al. 2010). Here a small reduction in extinction rate is apparent (∼5%), but this is no greater than the background extinction rate seen throughout the rest of the record. Some regions do indicate more substantial regional extinctions; for example, records from the U.S. Gulf Coast spanning the same interval indicate a significant decrease in palynological richness (Harrington & Jaramillo 2007). However, all of the taxa that disappear from this region are still found elsewhere during and following this event; the extinction is therefore local to regional rather than global.

Large-scale range shifts in plants are apparent at all scales—biome, continental, and regional—resulting in turnover of communities and the formation of novel plant assemblages. At the global scale, the most extensive range shift was that of the tropical biome, which extended to cover the terrestrial surface from the equator up to latitudes of 40° north and south (**Figure 3a**). In fact, this was the most extensive coverage of the tropical forest biome in Earth's history (Morley 2007, Willis & McElwain 2002, Willis et al. 2010a), as broad-leaved evergreen rainforest extended 20°–30° farther north compared with its present distribution (Wolfe 1985). Above 40° the forests became increasingly deciduous in their composition; mainly deciduous conifers and broad-leaved taxa were apparent on Antarctica (Morley 2007) and at the Arctic Circle (Taggart & Cross 2009). Many of the ecosystems created by this range shift were in novel in composition. In the Arctic, the high temperatures appear to have restricted boreal evergreen taxa to high-elevation refugia, and the lowlands were dominated by deciduous conifers and broad-leaved taxa. This polar deciduous forest was quite distinct from the extant boreal forest, as it had a notable absence of the evergreen Pinaceae family (Taggart & Cross 2009).
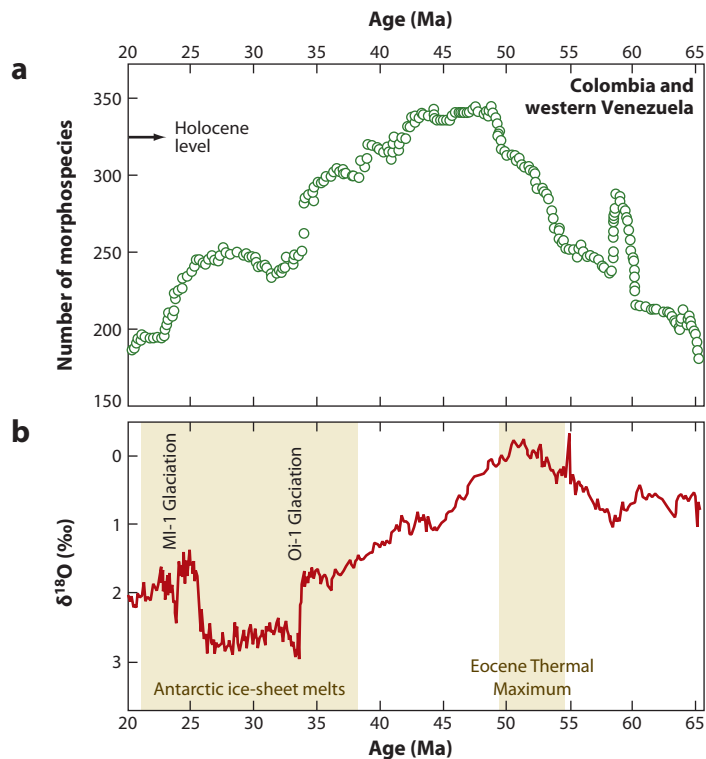
Figure 2

(*a*) Increase in diversity as represented in palynofloral diversity from sites in central Colombia and western
Venezuela between 65 and 20 Mya (redrawn from Jaramillo et al. 2006 and reprinted with permission from
AAAS). The number of morphospecies (*open circles*) is a measure of floral species richness estimated from
fossil pollen. (*b*) Also indicated are changes in $\delta^{18}O$ (from **http://www.ncdc.noaa.gov/paleo/metadata/
noaa-ocean-8674.html**), which are interpreted as reflecting changes in mean global temperature and total
global ice volume. During the time of the Eocene Thermal Maximum (marked in the figure), global mean
temperatures are estimated to have been up to 10°C warmer than present (Zachos et al. 2001, 2008).

Migration rates in response to warming at the PETM appear to have been rapid and com-
parable with those seen in early postglacial environments in the current interglacial (Wing et al.
2005). Plant fossils from several sites in Wyoming, North America, indicate that during the
10,000-year interval at the Paleocene-Eocene boundary a northern extension of floral ranges of
~450–2,200 km occurred. In addition, immigrants from both within the continent and other con-
tinents (particularly from Europe), combined with the persistence of the existing flora, resulted in
novel assemblages and an increase in overall species diversity.

Persistence therefore appears to have been the predominant response in the plant fossil record
for this warm interval in Earth's history. It is not possible to determine from the fossil record
alone the factors that enabled this persistence, but at least three adaptive features can be suggested.
First, many species had a much wider ecological tolerance than is apparent from their present-
day distributions, and thus they contain gene variations that enable tolerance of much higher
temperatures and water stress. This is probably the case for many tropical species (Jaramillo
et al. 2010) whose ancestors evolved during the late Cretaceous in much higher temperatures and
CO_2 levels. Second and closely related, higher levels of CO_2 induced an adaptive physiological
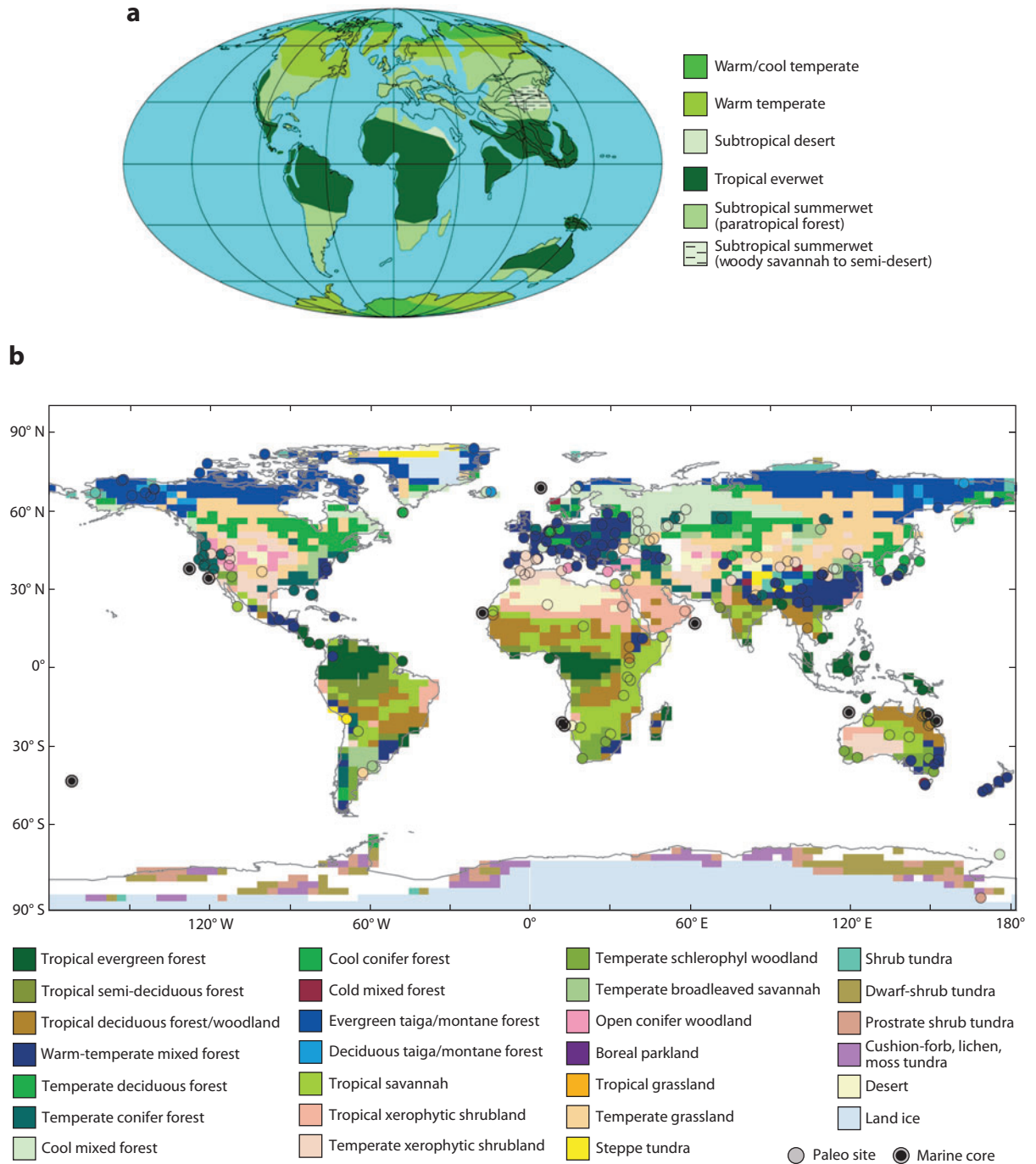response in the plants that enabled their persistence. A combination of modeling and experiments

a

Legend:
- Warm/cool temperate
- Warm temperate
- Subtropical desert
- Tropical everwet
- Subtropical summerwet (paratropical forest)
- Subtropical summerwet (woody savannah to semi-desert)

b

Legend:
- Tropical evergreen forest
- Tropical semi-deciduous forest
- Tropical deciduous forest/woodland
- Warm-temperate mixed forest
- Temperate deciduous forest
- Temperate conifer forest
- Cool mixed forest
- Cool conifer forest
- Cold mixed forest
- Evergreen taiga/montane forest
- Deciduous taiga/montane forest
- Tropical savannah
- Tropical xerophytic shrubland
- Temperate xerophytic shrubland
- Temperate schlerophyl woodland
- Temperate broadleaved savannah
- Open conifer woodland
- Boreal parkland
- Tropical grassland
- Temperate grassland
- Steppe tundra
- Shrub tundra
- Dwarf-shrub tundra
- Prostrate shrub tundra
- Cushion-forb, lichen, moss tundra
- Desert
- Land ice
- Paleo site
- Marine core

Figure 3

Range shift and distribution of the tropical biome during (*a*) the Eocene (56–50 Mya) (redrawn from Willis & McElwain 2002) and (*b*) the mid-Pliocene (redrawn from Salzmann et al. 2008). Circles indicate localities for paleobotanical data.

has indicated that in some plant groups, higher atmospheric CO_2 could increase carbon uptake through increased photosynthesis rates, resulting in enhanced net primary productivity (Lapola et al. 2009, Lloyd & Farquhar 2008, Woodward & Kelly 2008). In addition, plants compensate for water loss resulting from higher transpiration rates by reductions in stomatal conductance (Lloyd & Farquhar 2008). This process, often termed the CO_2 fertilization effect, may account for the observed increases in recruitment and growth rates in the Amazon and African forests over the past 30 years (e.g., Lewis et al. 2009). This may also account for the increase in the distribution and abundance of tropical rainforest in the PETM (Jaramillo et al. 2010). Third, those plants unable to adapt became restricted to small, microenvironmentally favorable refugia where they were able to persist; this certainly appears to have occurred for the evergreen Pinaceae family, as evidenced by its restriction to high-altitude locations during the PETM (Taggart & Cross 2009).

Despite evidence for such resilience during this interval, one of the main problems with these deep time records is that the ecological niche apparent for many species during the Eocene may not be representative of modern-day flora. Over the past 55 million years numerous lineage splits have occurred, and these may have resulted in a loss of genetic resilience. Recent genetic work indicates that many modern species have appeared since the beginning of the Miocene (Moritz et al. 2000, Pennington et al. 2004, Rull 2008). To examine whether a similar response in apparent in more recent populations, more recent time intervals are required. A key interval to examine in this respect is the mid-Pliocene geological stage, approximately 3.6–2.6 Ma.

3. MID-PLIOCENE WARM INTERVAL (3.6–2.6 MYR)

During the mid-Pliocene warm interval, estimates from various paleoclimatic proxies indicate that climatic conditions were, on average, warmer than the present day (Haywood et al. 2009, Jansen et al. 2007) and similar in many respects to those predicted in the next 50–100 years (Meinshausen et al. 2009). These included global temperatures up to 2–3°C warmer than present, atmospheric CO_2 between 360 and 440 ppmv (Zachos et al. 2001), and sea levels between 15 and 25 m higher than current levels (Dowsett & Cronin 1990). Similar to current and predicted future climate change, the greatest warming appears to have occurred in the high latitudes, as mean annual temperatures were more than 10°C higher than present (Salzmann et al. 2009). Summer temperatures in the Beardmore region of Antarctica, for example, are estimated to have been up to 16°C warmer than present (Francis et al. 2007). What were the biotic responses to this warmer climate?

In a recent synthesis of mid-Pliocene paleobotanical data from 202 terrestrial and marine sites, a response similar to that seen during the Eocene climatic optimum is observed (Salzmann et al. 2008, 2009). When data from these sites are integrated into a global information system platform, the overwhelming biotic response to this interval of warmth was clearly large-scale range shifts (**Figure 3b**). One of the most prominent changes was in polar and subpolar regions, where taiga with *Picea* and *Pinus* as the dominant species often replaced tundra forest (Salzmann et al. 2008, 2009). In the northern hemisphere high-latitude regions, this represented a range shift of ∼250 km in Siberia, 500 km in Alaska, and 2,500 km in the Canadian Arctic Archipelago (Salzmann et al. 2008). The transition zone between taiga forest and temperate cool and warm mixed forest was also located much further north; for example, the northward extension of temperate forests on the east coast of Canada was up 500–1,200 km (Salzmann et al. 2008). Novel forest assemblages dominated much of northern and central Europe with a mixture of cool-temperate deciduous taxa (e.g., *Fagus*, *Quercus*, *Ulmus*, *Tilia*) combined with warm-temperate and subtropical taxa (e.g., *Engelhardia*, *Liquidambar*, *Sequio*, *Taxodium*, *Gingko*, *Nyssa*, *Glyptostrobus*, *Magnolia*)

(e.g., Mai 1995, Thompson & Fleming 1996, Willis et al. 1999); presently these types are usually most closely associated with east Asian and North American affinities (Mai 1995).

Similarly in the Mediterranean region, a novel vegetation assemblage developed in which forests were dominated by Taxodiaceae with Ericaceae and trees of warm mixed forest (*Quercus, Carya, Pterocarya, Acer, Carpinus, Fagus*). The southern Mediterranean region had an increasing percentage of xerophytic vegetation (e.g., *Olea, Phillyrea, Pistacia, Ceratonia*), and tropical trees were apparent along the southern Mediterranean coasts (Jost et al. 2009). In the subtropics and tropics, tropical evergreen forests and mangroves persisted, but they also contained a mixture of rare and abundant tropical taxa and some temperate taxa for which no modern analogs exist.

In terms of overall diversity, during this warm interval no evidence is apparent for local, regional, or global plant extinctions. Rather, where studied, evidence supports an increase in diversity. For example, on the basis of pollen-type richness, an increase in overall rainforest diversity is apparent in southeast Asia, west Africa (e.g., Morley 2000, 2007), and several sites in South America (van der Hammen & Hooghiemstra 2000, 2003). In some regions, evidence from the pollen records suggests diversity considerably higher than the present day (Hooghiemstra & van der Hammen 1998; van der Hammen & Hooghiemstra 2000, 2003).

Biotic responses to this warm interval in Earth's history therefore include range shifts (mainly range expansions), persistence, novel assemblages, and increased diversity; there is no evidence for extinction. Why the opposite effect of that predicted in many models of future climate change is apparent requires once again a consideration of the influence of higher CO_2 levels combined with higher temperatures. Increases in CO_2 levels, in addition to inducing warming, will affect photosynthesis and ecosystem productivity (Norby et al. 2005, Woodward & Kelly 2008). Recent modeling has demonstrated that increased primary productivity has a linear positive relationship with diversity capacity such that a given ecosystem can support a greater number of species during intervals of higher CO_2 (Woodward & Kelly 2008). Interestingly, when results from this model are applied to future climatic scenarios, the output predicts enhanced plant growth, an increase in ecosystem productivity, and higher diversity (Woodward 2010). What is also apparent from this model, however, is that "weed" species for which migration is an insignificant barrier are likely to fill future diversity capacities. Thus, reduced population sizes owing to changing land-use patterns may still lead to extinctions, particularly of endemic species (Woodward & Kelly 2008). The temporal resolution and spatial resolution of the mid-Pliocene records are not sufficient to examine these proposed responses further; however, they can be addressed through examination of biotic responses to the two most recent interglacials, the Eemian and our current interglacial, the Holocene.

4. EEMIAN INTERGLACIAL (130,000–116,000 YEARS AGO)

Over the past 2 million years, a hallmark of the Earth's climate has been alternations between glacial and interglacial conditions. These transitions appear controlled by natural orbital variations and feedbacks that include increased high-latitude albedo and decreased concentrations of the greenhouse gases CO_2 and CH_4 during glaciations (Lambert et al. 2008, Petit et al. 1999). The amplitude of the climatic variations between glacial and interglacial conditions has increased over the past million years, and an ∼100,000-year periodicity has become dominant. The causes of the changes in CO_2 and CH_4 during glacial and interglacial episodes may relate both to carbon cycling by the oceans and to changes in terrestrial wetlands (Loulergue et al. 2008, Petit et al. 1999).

The last major interglacial, widely called the Eemian in Europe, occurred between ∼130,000 and 116,000 years ago and represents the last interval of extended warmth before the Holocene. In terms of understanding biotic responses to warmer climates, the Eemian is particularly interesting

because evidence from ice-core data suggests that global mean temperatures were ~2–4°C higher than present (Jansen et al. 2007), and high-latitude regions including Greenland and Antarctica exhibited even greater contrast, as estimated temperatures were up to ~5°C higher. In addition, sea levels were 6–9 m higher than today (Kopp et al. 2009), and the Greenland and Antarctic ice sheets were significantly smaller (Fleming & Lambeck 2004, Nicholls et al. 2011). The Eemian differed from the current interglacial, however, in terms of stronger effects of orbital forcing (Berger 1978). Greater obliquity and eccentricity caused an amplification of the seasonal cycle of insolation; summer insolation in the northern hemisphere was therefore significantly higher than today (Kaspar et al. 2005). Regional contrast in temperature distribution was also stronger. For example, Europe had a significant coast to interior gradient and a steep west-east gradient in winter temperature (Kaspar et al. 2005). Furthermore, atmospheric CO_2 was significantly lower than present; evidence from ice cores indicates a maximum atmospheric CO_2 level of 280 ppmv (Petit et al. 1999) in comparison with the current 390 ppmv.

In response to this warmer climate, the latitudinal extent of forests globally appears to have greatly increased. Evidence from plant DNA and amino acids from deep ice cores in Greenland, for example, reveals a high-latitude forest in southern Greenland during the Eemian indicative of a boreal ecosystem including *Alnus*, *Picea*, *Pinus*, and Taxodiaceae (Willerslev et al. 2007). Pollen evidence indicates that spruce was the dominant tree in these forests (Steig & Wolfe 2008). In mid-latitude (e.g., Kühl & Litt 2003) and low-latitude (e.g., van der Hammen & Hooghiemstra 2003) regions, forest also prevailed, although the composition of this forest differed notably from that of present. In a tropical record from Colombia, for example, the pollen from Eemian sediments indicates that *Weinmannia* forest dominated, in contrast to the *Quercus* forest that dominates in this region presently (van der Hammen & Hooghiemstra 2003). In mid-latitude regions differences were also noticeable in forest composition; many forest assemblages have no present-day analog (Kühl & Litt 2003). The composition of forest throughout Europe was much more uniform than present, and some species, such as *Tilia tomentosa*, had a much more widespread distribution than today [when it is confined to the Balkans and the Near East (Tzedakis 2007)]. *Carpinus* also dominated large parts of European deciduous forests. In comparison, the presence of *Fagus* was greatly reduced; populations were apparent only in southern Italy (Allen & Huntley 2009, Follieri et al. 1998, Magri 2010, Tzedakis 1994) in contrast to its extensive distribution in Europe and North America today (**Figure 4**).

A series of exposures from Indiana, Ontario, and New York in the midcontinent of North America has been provisionally dated as Sangamon (the North American equivalent of the Eemian) in age. Climate reconstructions from the sites suggest that during the warmest period temperatures may have been 1 to 2°C warmer than today and precipitation relatively high (Karrow et al. 2009). Winter conditions may have been milder and extreme cold events less frequent (Woodcock 1989). The fossil evidence from plants, mollusks, ostracodes, insects, and vertebrates suggests that the greatest diversity is in the lower sediments associated with the warmest conditions (Karrow et al. 2009). Palynological and plant macrofossil evidence also indicates significant range extensions of more southerly species such as *Maclura pomifera* (550 km), *Chamaecyparis thyoides* (200 km), *Quercus stellata* (120 km), *Robinia pseudoacacia* (110 km), and *Liquidambar styraciflua* (140 km) into Ontario as well as greater relative abundance of other southern taxa such as *Carya* in the northeastern Great Lakes region (Karrow et al. 2009, Woodcock 1989). Interestingly, the synchronous occurrence of high tree and herb diversity during the warmest period comes from a period with little fossil charcoal, which suggests limited disturbance and canopy opening via fires (Karrow et al. 2009).

The generally high biodiversity and remarkable resilience of all vegetation types during the Eemian are important. As far as it is possible to ascertain from the plant fossil record, nothing

a Present range
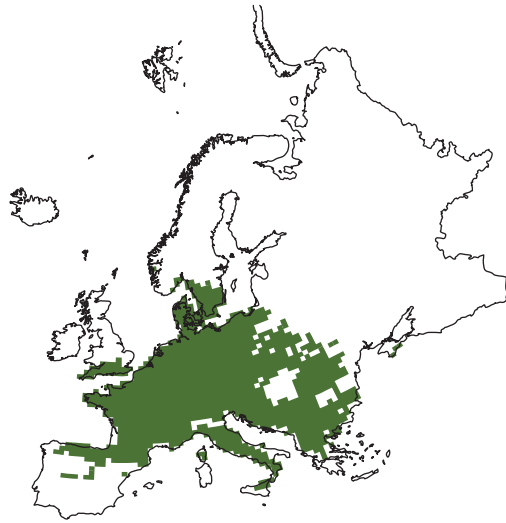
b Range during Eemian interglacial

Figure 4

(*a*) Present-day distribution of *Fagus sylvatica* in Europe (redrawn from Atlas Flora Europaea). (*b*) Distribution of *Fagus sylvatica* in Europe during the Eemian interglacial; its presence is noted only in southern Italy (Allen & Huntley 2009, Magri 2010, Tzedakis 2007). Distributional range during the Eemian is ~2% of that seen during the current interglacial.

went extinct despite these significantly higher temperatures and, for some species, greatly reduced distributional ranges. McFarlane et al. (1998) suggested that Eemian warming may have led to the extinction of the West Indian megarodent *Amblyrhiza inundata*, owing to a reduction in island land area caused by the extremely high magnitude of eustatic sea level rise during that time. There is evidence, however, for a far greater number of extinctions within the Pleistocene assemblage of Eurasia at the close of the Eemian, likely owing to subsequent glacial cooling and range displacement (Pushkina 2007, Svenning 2003).

So what information can be obtained from these Eemian records in terms of understanding persistence and resilience to future climate change? The first is that, as predicted by species-envelope models for current and future climate change, the overall composition of forests will probably alter; some species will increase in dominance, and others will lose abundance. An interesting example at the southern edge of Europe is the decline in *Fagus* that has been recorded with significantly lower recruitment observed since 1973. The reason for this decline is thought to be a combination of warming temperatures and a lack of increase in precipitation (Jump et al. 2006). Tzedakis (2007) suggested that lack of precipitation during the Eemian might have inhibited the expansion of *Fagus*. Species that were unable to unable to adapt to the warmer temperatures and/or decreased precipitation therefore appear to have become restricted to refugial regions where local climatic conditions or reduced competitive interactions meant that they were able to persist. For *Fagus* this represented an ~98% reduction in its distributional range in comparison with its present-day distribution (**Figure 4**). Despite this dramatic reduction in the so-called climate space, this species appears to have been capable of expanding from extremely low-density populations (less than 2% of its current range) to become a dominant tree in many central European forests in the current interglacial. Persistence that enabled species to remain in situ as well as movement to suitable climate space seems to have occurred throughout the Eemian. What still needs to be considered,

however, is whether the predicted rate of climate warming will have an overriding influence; i.e., is the rate too rapid for plants to respond and/or move to suitable climate space? To further address these questions it is necessary to look at the most recent records, including the rapid warming that occurred at the transition to the current interglacial.

5. LATE GLACIAL-POSTGLACIAL TRANSITION INTO THE HOLOCENE

Triggered by increasing summer insolation in the high latitudes of the Northern Hemisphere, the last transition between glacial and interglacial conditions commenced following the Last Glacial Maximum (LGM; ~20 ka) of the Pleistocene and continued through important changes such as the final disappearance of the Laurentide Ice Sheet in northern Canada, eustatic rise in sea level as the ice melted, and increasing temperatures. These events extended into the middle Holocene at approximately 6 ka. Owing to declining summer insolation in the Northern Hemisphere in many but not all regions, a general cooling has occurred since approximately 6 to 4 ka.

Five factors make the glacial-interglacial transition and the early to middle Holocene particularly relevant to anticipation of the potential impacts of global warming on biodiversity. These are:

1. Similar to current warming, the glacial-interglacial transition represents a global climatic change that had repercussions from the tropics to the high latitudes.

2. The difference in global average annual temperature between glacial and interglacial conditions of 3.5 to 5.2°C is of similar magnitude to anticipated twenty-first century warming (Solomon et al. 2007).

3. Not only did temperatures significantly warm during the Holocene relative to the LGM, but as is the case for anticipated future warming, climatic conditions developed during the Holocene warming that had no analog during the LGM (Williams et al. 2007).

4. Estimates of rapid warming coming into the Holocene are roughly comparable with estimates of warming over the twenty-first century (Solomon et al. 2007). In mid- to high-latitude regions, for example, a relatively abrupt warming occurred between 15 and 14 ka that was centered at 14.7 ka. In Greenland this was the fastest rate of warming during the transition, and temperatures may have risen by 10°C in a few years (Steffensen et al. 2008). In the Swiss Alps and other parts of Europe, a warming of 2 to 5°C appears to have occurred in 200 years or less (Lotter et al. 2011). In the Sierra Nevada of California, rates of warming in the late glacial may have been 4 to 5°C every 500 years between ~15 ka and 14 ka (MacDonald et al. 2008c). In addition, during the last transition the overall warming was punctuated by the rapid cooling of the Younger Dryas Stadial (~13.5 to 11.5 ka) followed by extremely rapid warming. At the higher latitudes of the Northern Hemisphere, the rapid warming at ~11.7 to 11.5 ka produced increases of 5°C and more over a few decades (Kobashi et al. 2008). Data from Greenland ice cores suggest that a >10°C warming may have occurred in a period of 20 to 60 years (Steffensen et al. 2008). A similarly rapid rate of climate change also has been recorded in low-latitude regions. Evidence from Lake Masoko, East Africa, indicates an equally dramatic climate change coming out of the Younger Dryas, but this change has been interpreted as a rapid increase in precipitation and/or temperature (Garcin et al. 2007). In California, which is far distant from the Younger Dryas' North Atlantic nexus, warming at the close of the Younger Dryas may have been on the order of 3°C in less than 100 to 200 years (MacDonald et al. 2008c). For the entire Southwest a general warming of approximately 4°C may have occurred in less than a century

(Cole 2010). For comparison, warming in western North America may be on the order of 3.5 to 4°C over the twenty-first century (Solomon et al. 2007).

5. The amount of CO_2 in the atmosphere increased from approximately 180 ppmv during the glacial to 280 ppmv during the interglacial, and this would have resulted in changes in photosynthetic activity and plant stomatal density that are expected to influence functioning, such as moisture use efficiency (Bennett & Willis 2000).

What is the evidence for biodiversity changes during the Pleistocene-Holocene transition? At this time little evidence supports significant plant species extinction during the warming (Willis et al. 2010b). One well-known exception is the loss of the spruce species *Picea critchfieldii*, which was common in the southeastern United States until approximately 15 ka (Jackson & Weng 1999). However, the exact timing of the ultimate extinction of the species and the role climate warming may have played remain unknown. Although this review is largely concerned with plants, an incredible loss of large mammal species occurred in the Americas and northern Eurasia during the Pleistocene-Holocene transition, and this warrants some comment. In North America more than 30 genera of large mammals including horses, camels, mammoths, and mastodons were lost (Haynes et al. 2009). In South America 100% of mega mammals (species > 1,000 kg) and 80% of large mammals (>44 kg) went extinct (Haynes et al. 2009). Typical extinction rates during the earlier Pleistocene may have been on the order of 1 extinction per 40,000 years and accelerated to the equivalent of 1 extinction per 30 years at the early Pleistocene-Holocene transition. However, as clear as the concurrence seems to be, it is difficult to ascribe the massive losses of large mammals to warming specifically (Haynes et al. 2009, Johnson 2009, Koch & Barnosky 2006).

In response to the rapid climate change, the predominant response in the plant record across the globe appears to have been one of ecological turnover and range adjustment. In the tropics, for example, there are numerous examples of a rapid switch in forest composition. One of the best data sets is from Lake Masoko in East Africa (Vincens et al. 2007). Here the record indicates a switch from forest dominated by taxa intolerant of a dry season to forest dominated by taxa tolerant of a dry season in less than 100 years (Vincens et al. 2007). Similarly rapid response rates to climate warming are also seen throughout mid- to high-latitude sites (Williams et al. 2002, Willis et al. 2010b). Vegetational responses recorded in 11 sedimentary sequences with a suitably high temporal resolution from around the North Atlantic region, for example, indicate a change in forest composition in less than 100 years (Williams et al. 2002). The change in forest composition depended upon region. In central Europe, for example, there was a change from needle-leaved to broad-leaved deciduous forest (Feurdean et al. 2007, Willis et al. 1997), whereas in higher latitudinal regions, closer to the ice sheets, a rapid expansion of herbaceous and shrub flora occurred (Birks & Birks 2008), and in some cases local tree species expanded from their refugial populations (e.g., *Betula*, *Pinus*, *Picea*). These became established within a century, which suggests climate-driven ecosystem changes rather than gradual plant succession on newly deglaciated land (Heikkilä et al. 2009).

In addition to in situ compositional turnover, large-scale range shifts occurred into mid- to high latitudes. The relatively widely accepted assumption that plant migration rates during the Pleistocene-Holocene transition kept pace with climatic changes is still a topic of debate for some (e.g., Svenning & Skov 2007), suggesting that the current geographic distribution of the diversity of temperate tree species in Europe can be correlated with distance from likely glacial refugia and thus reflects, at least in part, extremely slow postglacial migration rates and the inability of some species to reach their climatic limits over the course of the Holocene. However, there are also numerous records of widespread refugial plant populations in central and northern Europe (e.g., Binney et al. 2009), and for these species, the response to warming would have been more a case of

expansion through diffusion by their widespread refugial populations rather than northerly range shifts (Bhagwat & Willis 2008, Birks & Willis 2009).

Postglacial plant migration rates reconstructed from pollen records can be compared with the migration rates likely to be required for species to remain in their climatic envelopes over the twenty-first century. The rates required to adjust ranges to late twenty-first century climate spaces are often much faster than those demonstrated using fossil records (e.g., McLachlan et al. 2005) and/or observations of recent range adjustment (Clark et al. 2001). The reconstructed rates of plant species' range adjustments typically range from 100 to 2,000 m year^{-1} (MacDonald 1993, McLachlan et al. 2005). However, these rates may be overestimates. Recent genetic analysis of the geography of modern-day genetic variations in plant species suggests that fossil pollen–based reconstructions may be insensitive to the preexisting presence of sparse populations across wide areas and thus overestimate actual rates of range adjustment (Anderson et al. 2006, McLachlan et al. 2005). For example, Ritchie & MacDonald (1986) used fossil pollen records to estimate migration rates for the southward spread of white spruce (*Picea glauca*) into newly deglaciated portions of Canada and Alaska on the order of 2,000 km in 1,000 years. However, more recent genetic analysis of modern spruce populations (Anderson et al. 2006) suggests that small refugial populations of white spruce likely survived in Alaska and/or the Yukon during the LGM and would have provided a local source for colonization in the north. Thus, the high estimated rates of northward migration may be spurious. Interestingly, the growing evidence for long-term persistence of widely scattered and isolated small populations of plants during the LGM (Binney et al. 2009) has generated the observation that such populations today may provide a means of rapid response to future climate change in areas that will become more amenable to support of a species, or may indicate that small populations may be able to survive in particular local settings in areas that become generally unfavorable for support of the species (Bhagwat & Willis 2008, Birks & Willis 2009, Pearson 2006).

As a final point on rates of plant migration, it is notable that although the northern tree line regions of North America and Eurasia have warmed appreciably over the twentieth and early twenty-first century, and although some northern tree populations have increased in density, there is little evidence of northward range extension among tree line conifer genera such as *Picea* and *Larix*. Indeed, in several cases the ranges have not yet fully reoccupied areas that these genera inhabited during the medieval warm period approximately 1,000 years ago (MacDonald 2008b, 2010; Payette 2007). Given the life history of far northern conifers in terms of reproductive age and growth rates, it is difficult to envision that they will expand to their estimated 2100 climate limits within the next 90 years (MacDonald 2010).

There is no clear evidence of plant speciation in response to the warming at the Pleistocene-Holocene transition. Holocene palynological, plant macrofossil, and ancient DNA records do, however, provide insights into the relationship between warming and local to regional changes in plant biodiversity that may be useful in anticipating future changes. Although fossil pollen taxon richness is not a direct proxy for plant species richness (Weng et al. 2006), palynology can be used to infer plant diversity.

In the case of northern Europe, evidence from the rarefaction analysis of fossil pollen records suggests that a diverse herb and small shrub flora that was an admixture of tundra and steppe elements developed during the warming of the early transition (Berglund et al. 2008a,b). By approximately 9.5 ka, several of these late glacial taxa disappeared, and a relatively species-poor boreal flora was established. However, as the Holocene proceeded, the diversity increased as a more nemoral flora developed through addition of southern elements (Berglund et al. 2008a,b). This pattern of increasing diversity continued until the development of widespread agriculture and replacement of native vegetation during the medieval period. As the relatively slow growth

in species diversity during the mid-Holocene does not seem to correlate with any strong climatic trends, Berglund et al. (2008a,b) have suggested that the progressive, but slow, increase in nemoral elements largely reflected slow migration of species from the south into northern regions. A similar pattern of relatively diverse late glacial and early postglacial assemblages giving away to less diverse conifer and birch forest is reported in Switzerland (van der Knaap 2009). A transitional peak in diversity and taxon evenness is present during the early transition when elements of the late glacial herb and graminoid vegetation are present along with elements from later juniper-, birch-, and pine-dominated stages (van der Knaap 2009).

In high-latitude regions, a similar increase in diversity is detected in the early postglacial with increasing warmth and moisture (Birks & Birks 2008, Heikkilä et al. 2009). Here this diversity rise was the result of either an increase in herbaceous and shrub flora (Birks & Birks 2008) or expansions of local tree species from their refugial populations (Heikkilä et al. 2009). The addition of these species to the existing arctic flora that persisted into the early postglacial resulted in an increase in overall diversity. Similarly, analysis of ancient DNA recovered from permafrost soils in Siberia shows a pattern of low plant species diversity in the LGM and increasing diversity into the early Holocene (Willerslev et al. 2003). The high plant diversity was maintained to the late Holocene in this case.

One of the most interesting records from low-latitude regions is from the Sahara desert, where fossil pollen evidence shows that increasing moisture availability coincident with early Holocene warming led to increasing plant diversity after 12.5 ka (Watrin et al. 2009). During this greening of the Sahara, diversity reached a maximum at approximately 8.5 ka when Saharan/Sahalan elements were mixed with savannah and forest species of Guineo-Congolian, Guineo-Sudanian, and Sudanian affinities from the more humid south. Some of the southern species occurred more than 400–500 km north of their present ranges, and the mixed xeric-semimesic-mesic vegetation of that time has no modern counterpart (Watrin et al. 2009). Increasing aridity, largely because of late Holocene cooling, led to widespread extirpation of nonxeric species from much of the region and the development of the low biodiversity typical of today.

Packrat records from the arid regions of Southwestern North America contain diverse assemblages of plant macrofossils and can be used to infer floristic changes during the Pleistocene-Holocene transition and post-Younger Dryas warming (Cole 2010). Similar to the pollen records from Europe, these records suggest a complex set of changes in regional biodiversity in response to warming. Plant diversity declined during the abrupt warming (~4°C over a century) and increasing aridity at approximately 14.7 ka (Cole 2010). However, influxes of successional species eventually caused an increase in diversity as the Holocene progressed. Different species appear to have responded at different rates to the abrupt warming, and this led to a 2,700-year period of mixed vegetation of early and later arriving species.

The record of diversity changes during the Pleistocene-Holocene transition therefore suggests that different patterns may develop dependent upon regional context; given sufficient moisture along with warming, higher biodiversity can be the end product. However, transitional communities with either lower or higher diversity can form as biodiversity adjusts to warming. In particular, the individualistic responses of plants to warming and associated climatic changes in terms of physiological functioning, rates of migrational response, or rates of extirpation can produce communities that are novel compared with previous or subsequent assemblages and can be strictly transitional.

In summary, several interesting observations result as biotic responses to climate warming emerge from the Holocene fossil evidence. Despite fast rates of warming that in some cases (14.7 ka and post-Younger Dryas) are close to the anticipated rates and magnitudes of change for the next 100 years, there is little evidence for plant extinction or speciation. There is, however,

evidence of large mammal extinction, but several factors were probably at play in bringing about this event. The migration rates of many species will be too slow to enable range shifts that keep pace with climate change. However, evidence also suggests remarkable persistence under unfavorable conditions before local extinction. This can give rise to transient diversities that are either higher (resulting from an admixture of new arrivals and preexisting species on their way out) or lower (slow migration of new species into the area) than will occur under final equilibrium with climate.

6. CONCLUSIONS

Persistence and range shifts (migrations) seem to have been the predominant terrestrial biotic response (mainly of plants) to warmer intervals in Earth's history. The same responses also appear to have occurred during intervals of rapid climate change. Local extinctions certainly took place during intervals of warming, but evidence for global extinctions or extinctions resulting from reduction of population sizes on the scale predicted for the next century owing to loss of suitable climate space (Thomas et al. 2004) is not apparent. One line of argument may be that the fossil records are too crude in terms of taxonomic resolution and therefore are not detecting declines. However, this does not appear to be the case for other intervals in Earth's history. For example, at the start of the Pleistocene ice ages (Pushkina 2007, Svenning 2003), the fossil record offers clear evidence for numerous extinctions associated with climate cooling. A low level of extinction in response to climate warming from the fossil record is probably, therefore, fairly well representative of what occurred, although some endemic populations with narrow ecological tolerances (and poor representation in the fossil record) likely went extinct without notice.

In terms of migrations, for all intervals examined, numerous examples indicate range shifts occurring in response to climate warming. However, also apparent is that many plant species do not have the ability to move as quickly as their climate space, a point recently highlighted as of particular concern for many plants with future climate change (Loarie et al. 2009). Rather, a persistence of the biota in its original location, usually with a greatly reduced population size, and/or a lagged migrational response to the climate change (e.g., Svenning & Skov 2007), appears to occur. Another factor leading to persistence appears to have been the survival of populations in small, environmentally favorable refugial localities, as seen for many European alpine species during the mid-Holocene climatic optimum (Birks & Willis 2009).

Another key point to emerge from these records is that novel ecosystems are the norm during intervals of climate change rather than the exception (Seastedt et al. 2008, Williams et al. 2007). The increased diversity and turnover during the warming combined with immigration of new species and persistence of existing species resulted in plant assemblages that have no present day analog.

What do these long-term ecological records mean for future climate change conservation strategies? Does this mean that the threats of future climate change are overstated? If concerned with climate change alone, this conclusion could be valid for many terrestrial plants, as their fossil records display a far greater ecological tolerance and persistence to climate warming than often has been ascribed. However, given the double cocktail of rapid climate change and greatly reduced range sizes owing to anthropogenic activities (Travis 2003), there is certainly no room to be complacent. Rather, conservation strategies should become more closely aligned with those factors that are known to enable persistence. These include identification and protection of important refugial regions, maintenance of diverse communities and genetic diversity within species, and the acknowledgment that even small populations outside of their perceived ideal climate space may persist and are therefore worthy of conservation. Finally, a new set of conservation measures should be developed for novel ecosystems (Seastedt et al. 2008) because, if history is correct,

they will become the norm and should be viewed as something to be conserved rather than resisted.

DISCLOSURE STATEMENT

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