
Terrestrial Biosphere Dynamics in the Climate System: Past and Future

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5.1 Introduction

The terrestrial biosphere is one of the most critical and complex components of the climate system, regulating fluxes of energy, water and aerosols between the earth surface and atmosphere. The terrestrial biosphere also is central to the biogeochemistry of our planet, particularly with regard to the global carbon and nitrogen cycles. Prediction or assessment of future earth system change will always be limited, to some degree, by our ability to define how the terrestrial biosphere will respond to altered climatic forcing, and how this response will express itself as biophysical and biogeochemical feedbacks. The terrestrial biosphere plays more central roles in the health of the planet via biodiversity and ecosystem services (i.e. benefits to society). The exact dimensions of these roles are difficult to define, but there is no doubt that a premium must be placed on maintaining biodiversity, as well as the health of ecosystems critical for human sustainability.

Given the large magnitude of projected future (e.g. 21st century) climate change, it is simply not possible to make realistic assessments of future regional climate or biogeochemical ecosystem and biodiversity responses, without turning to the record of past climate and ecosystem change. Just as study of the contemporary biosphere is essential for understanding short-term biosphere dynamics, paleoenvironmental research provides the only way to observe and understand how the biosphere responds to climate change on decadal and longer timescales. Moreover, the paleoenvironmental record contains the only data relevant to understanding biosphere dynamics in the face of large climatic change and in the absence of significant anthropogenic influences. Because many aspects of future change are likely to

be without 20th century or even geological analogs (Crowley 1990, Webb 1992), assessments of future conditions will, by necessity, be increasingly based on numerical process models. As with other areas of environmental science (e.g. climate prediction), this means that we must also turn to the paleoenvironmental record to evaluate the realism of predictive models. It is not possible to assess future change without a complete understanding of past change, and how well we can simulate it.

The purpose of this chapter is to synthesize the remarkable progress that has recently been made in understanding the role and response of the terrestrial biosphere in the face of climatic change. We first examine the biogeochemical and biophysical roles that the terrestrial biosphere has played in the context of past climate change, and what these roles mean for the future. Realistic biospheric dynamics appear to impart significant positive climate feedbacks, and thus will likely amplify future changes in temperature, precipitation, and other climate variables. The terrestrial biosphere has also played a significant role in modulating atmospheric trace-gas and aerosol concentrations through time. Here, the emphasis is on the Late Quaternary, where we have a rich, well-dated record of large-scale climatic change, but we also place biosphere dynamics in a longer-term context. Although our synthesis emphasizes vegetation change, particularly in the more heavily studied northern extratropics, we also consider past responses of animal populations. The implications of our synthesis are global.

The primary thesis of this chapter is that the terrestrial biosphere has evolved in concert with significant large-scale climatic change during the Quaternary. The magnitude, rate and “destination”

of climate and atmospheric trace-gas composition change can define an “envelope of natural variability”. By “destination”, we mean the exact configuration of the climate system, including atmospheric composition, at a particular point in time. Over the last several hundred thousand years, the magnitude, rate and destinations of the climate system have, remarkably enough, stayed within some clear bounds. Thanks to recent advances in paleoceanography and ice-core paleoclimatology (see Chapters 2-4), we know many details of atmospheric composition, climate forcing, and climate response for the last 450,000 years (Figure 5.1). We also know that this period, encompassing four major glacial-interglacial cycles, is more or less representative of the last million years of earth history (Imbrie et al. 1993; Chapter 3). Although the spatial configuration of seasonal insolation and ice sheets varied through time with changes in the earth’s orbit, both seasonal insolation and the total volume of land ice varied within well-defined limits. Glacial ice sheets grew repeatedly over large regions of North America and Eurasia, lowering global sea level substantially as they did so. However, the glacial ice sheets appear to have never grown more than it takes to lower global sea level by 130 m below today’s level (Imbrie et al. 1993, Chapter 3). During the many intervening warm interglacial periods, global ice sheets almost always retreated to configurations (i.e. extent and height) similar to, or slightly smaller than, those of today. Melting of Greenland and Antarctic ice sheets at these times rarely produced more than about 5 meters of sea level rise above today’s level (Cuffey and Marshall 2000, Lambeck and Chappell 2001). Similarly, everything that is known about atmospheric trace-gas concentrations suggests that they were tightly bounded within the natural envelope over the last several million years; for example, CO₂ varied naturally between about 180 and 300 ppmv (Figure 5.1, Petit et al. 1999), and probably stayed close to modern levels much farther back in time (i.e. even back to 25 Ma) (Zachos et al. 2001). Thus, extant life on earth (i.e. species and ecosystems) has evolved within a fairly well-defined envelope of climate variability

There are clear signs that anthropogenic climate forcing is driving the earth’s climate to destinations well outside the natural envelope (e.g. unprecedented global warmth of the late 20th century) (Overpeck et al. 1997, Mann et al. 1998, Crowley 2000, Huang et al. 2000, Jones et al. 2001.) (cf. Chapter 6). For example, ambient levels of many atmospheric trace-gas constituents (e.g. 370 ppmv for CO₂ in AD 2000) already exceed those recorded in ice cores for the last 420,000 years, and are likely

to continue their unprecedented growth (IPCC 2001). At local to regional scales, species and ecosystems in some parts of the world could experience a sustained period of climatic conditions unlike any experienced in the last million or more years (e.g. warm temperatures and increased potential evapotranspiration).

In the face of large future atmospheric composition and climate changes, aspects of the terrestrial biosphere will likely change in ways not seen in the Quaternary. Moreover, just as the future mean climate of many regions is projected to be well outside the natural envelope, it is possible that the variability shifts and rates of change associated with future climate change could also exceed the natural bounds of the last million years (Figure 5.2) (Jackson and Overpeck 2000). The attendant biotic response will take years to fully adjust, thus making it difficult to estimate biospheric feedbacks to the atmosphere in the coming decades. Projected future climate and atmospheric changes will also have significant deleterious impacts on biodiversity and basic ecosystem services, particularly when other anthropogenic stresses (e.g. land-use, invasive species, water depletion and pollution) are factored in. Moreover, the specter of unanticipated climate changes or “surprises” (Broecker 1987, Overpeck 1996, Overpeck and Webb 2000, National Research Council 2002) suggests that reliable prediction of regional climate, and thus of terrestrial biosphere change, will be difficult.

5.2 The roles of the terrestrial biosphere in the climate system

The terrestrial biosphere presently serves as a major net sink of atmospheric carbon, sequestering nearly 30% of total annual anthropogenic carbon emissions (ca. 8 Gt total) each year over the last decade (Watson et al. 2000). Given the enormous size of the terrestrial carbon pool (2500 Gt, distributed 20% in vegetation and 80% in soils and detritus; Schimel et al. 1996), change in the terrestrial biosphere has the potential to play an even larger role in global carbon cycle dynamics in the future. Assessing this role will require a better understanding of how the terrestrial biosphere will respond on local to global spatial scales in the face of significant climate change. However, the growing focus of attention on the terrestrial biosphere goes well beyond carbon dioxide, to the role of terrestrial vegetation in a range of climatically-sensitive biogeochemical and biophysical processes. The purpose of this section is to briefly discuss these processes from a paleoenvironmental perspective, and to highlight research needed to improve future assessments. Although the

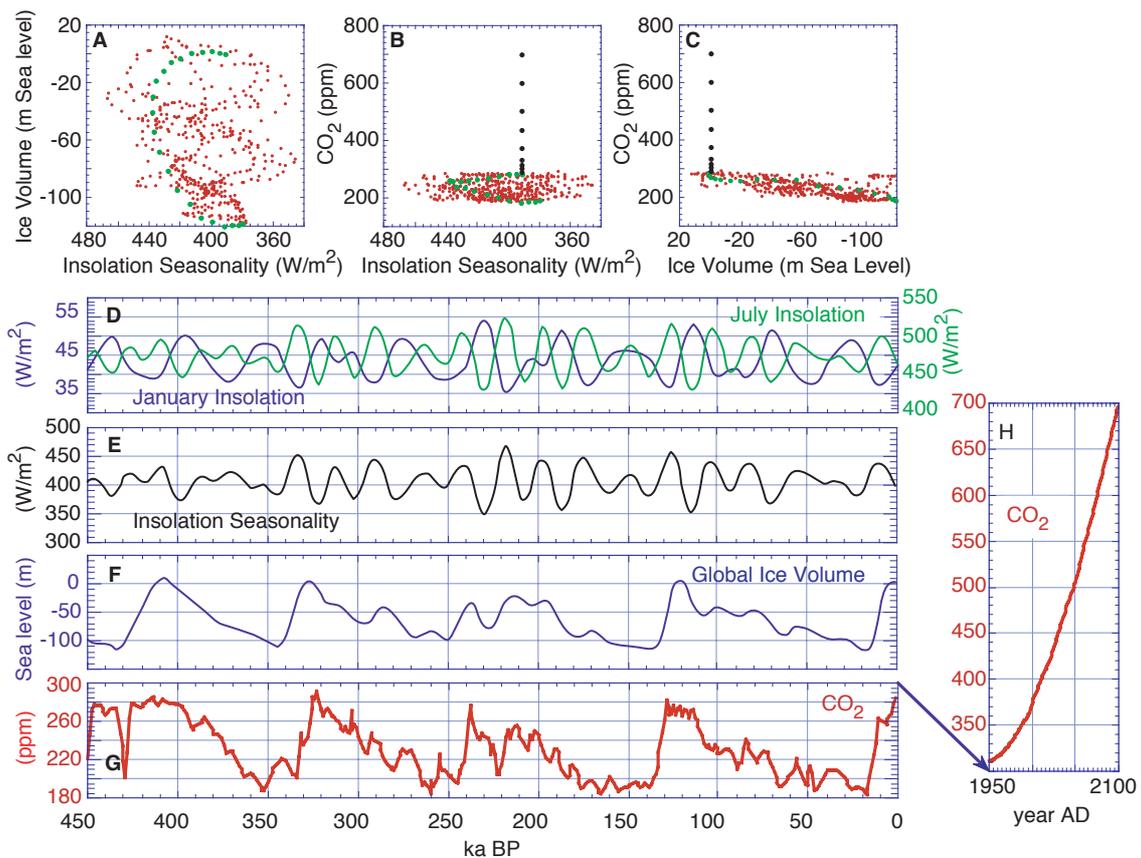


Fig. 5.1. Major climate forcing for the last 450,000 years (observed at 1000-year intervals to 1950), and for the period 1850 to 2100 (observed and projected at 25-year intervals). Scatter plots (A-C) and time series (D-H) of glacial ice volume (in meters of sea-level equivalent, see below), insolation at the top of the atmosphere (January, July and July minus January (“seasonality”), all calculated for 60°N (Berger and Loutre 1991), and atmospheric CO₂ concentration (Etheridge et al. 1996, IPCC 2001, Petit et al. 1999, Robertson et al. 2001). Note that CO₂ levels projected for the next century (red line in H, and black dots in A-C (IPCC 2001) are plotted versus years A.D. rather than B.P. Glacial ice volumes were obtained using the global average deepwater (“benthic”) $\delta^{18}\text{O}$ (Imbrie et al. 1992) scaled to a 20,000 years B.P. glacial to present (interglacial) sea-level amplitude equal to the observed value of 120m (Fairbanks 1989). The trajectory (*sensu* Bartlein et al. 1997) of climate forcing over the last 21,000 years is displayed as green dots (A-C). Whereas atmospheric trace gas (e.g. CO₂) levels are expected to increase dramatically to unprecedented levels in the next century (A-C, H), both insolation and global sea level are not likely to change much relative to recent geologic variations. Figure from Jackson and Overpeck (2000).

last decade has seen great strides in identifying the roles played by the biosphere, the next decade will see a greater focus on quantifying these roles in the face of global climate change.

5.2.1 Biogeochemical roles

In the last decade, the history of atmospheric CO₂, CH₄ and (to a lesser extent) N₂O concentrations over recent earth history (i.e. the last 450,000 years, Figure 5.1) has become well articulated (Blunier et al. 1995, Indermühle et al. 1999, Petit et al. 1999, Monnin et al. 2001) (Chapter 2). This work reveals that trace-gas concentrations have stayed within well-defined limits, and thus define a natural envelope of atmospheric composition variability within which the earth’s present biosphere evolved. As chapters 2 and 4 detail, however, much remains to

be done in terms of understanding the mechanisms responsible for past trace-gas change, and in particular, the roles played by terrestrial plants and soils. On these long timescales, the terrestrial biota combined with oceanic processes to drive the large observed variability in atmospheric CO₂ and N₂O, whereas the observed changes in CH₄ were likely due almost entirely to changes on land with the possible exception of rare marine sediment methane hydrate instability (Kennett et al. 2000).

To simulate past trace-gas variability, we must first simulate the regional patterns of vegetation and soil response to past climate change in a realistic manner. The same holds true for simulating past changes in natural tropospheric aerosols. Vegetation serves as the primary stabilizer of soils and thus a key player in the modulation of natural “dust” aero-

sols (Pye 1987, Mahowald et al. 1999, Kohfeld and Harrison 2000, Mangan et al. in press). Similarly, aerosol and particulate emissions as a result of biomass burning play an important feedback role in the climate system (Levine 1991, Clark et al. 1996, Levine 1996a, 1996b, Watson et al. 2000). Whether derived from mineral or biomass sources, aerosols can have important biogeochemical, ecological and climatic impacts (Levine 1991, Penner et al. 1992, Levine 1996a, Levine 1996b, Overpeck et al. 1996, Avila and Penuelas 1999, Chadwick et al. 1999, Chapin et al. 2000, Shinn et al. 2000, Loreau et al. 2001). The important point here, however, is that it will be difficult to assess the mechanisms of past (or future) aerosol variability without first understanding how regional-scale vegetation and soils respond to climate change.

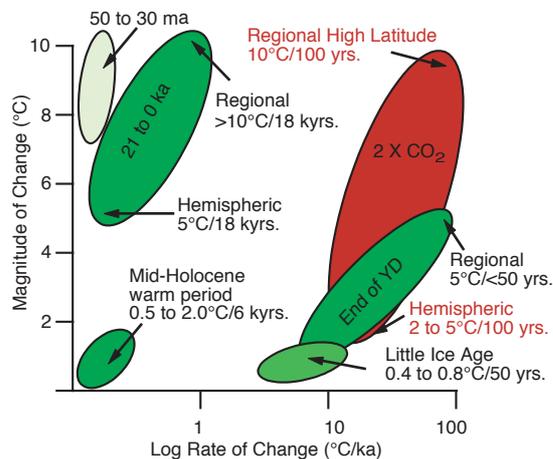


Fig. 5.2. Summary comparison of the rates and magnitudes of possible future climate change (estimated in terms of mean annual temperature) with those associated with several well-known periods of past change in regions that were vegetated. Rates of future regional temperature change could far exceed any widespread change in the late Quaternary (updated after Jackson and Overpeck 2000 using Zachos et al. 2001).

5.2.2 Biophysical roles

An understanding of the role of terrestrial vegetation in biogeochemical cycles is detailed in Chapters 2 and 4, but there is also reason to focus on the critical biophysical roles played by vegetation in the climate systems (i.e. in modulating energy, water, and momentum fluxes). Only 15 years ago, most studies focused on how vegetation change affects climate via changes in land-surface albedo. In contrast, the climate modeling community now considers a range of terrestrial feedbacks in addition to albedo, including evapotranspiration, surface

roughness, and snow masking (Hansen et al. 1984, Rind 1984, Hayden 1998, Eugster et al. 2000). Paleoenvironmental studies are the only source of long observational records of past vegetation, ocean, and climate change, and thus provide a unique opportunity to learn about the nature of these feedbacks, and also to evaluate how well we model them.

Biophysical climate feedbacks have long been a focus in the study of low-latitude climate variability. Deforestation in the Amazon and its associated climatic impacts are richly debated (e.g. Nobre et al. 1991, Dickinson and Kennedy 1992), just as are the 20th century biophysical (land-surface) feedback dynamics of the Sahel and North African climate (Charney 1975, Xue 1997, Zeng et al. 1999, Nicholson 2000, Wang and Elfatih 2000). Over the last decade, it has become clear that land-surface feedbacks have also been an important amplifier of climate sensitivity in the tropics and sub-tropics over the late Quaternary. Street-Perrot et al. (1990) highlighted the role of North African land-surface albedo change as a key positive feedback in the early Holocene, and this work has led to a host of studies focused on quantifying the role of this feedback in amplifying the radiative changes associated with Milankovitch forcing (Kutzbach et al. 1996, Coe and Bonan 1997, Broström et al. 1998). In a large community effort (the Paleoclimate Modeling Intercomparison Project, PMIP, Joussaume et al. 1999) a set of mid-Holocene simulations (made with 18 different global climate models) was compared. The conclusion of this comparison was that all of the models significantly underestimated the full magnitude of hydrologic changes needed to match the observed changes for that period – a result of the fact that all of the simulations lacked key feedbacks, including vegetation-climate interactions (Figure 5.3). More recent simulations with interactive vegetation and/or ocean dynamics have subsequently shown that these feedbacks do indeed help constrain North African climate sensitivity during the Last Glacial Maximum (ca. 20ka) and Holocene (Figure 5.3) though further improvements are clearly needed (Claussen and Gayler 1997, Kutzbach and Liu 1997, Texier et al. 1997).

The last decade has also seen significant work investigating land-surface (vegetation) biophysical feedbacks at high latitudes; not surprisingly, these feedbacks are dominated by the interaction of vegetation, snow, and temperature (Bonan et al. 1992, Eugster et al. 2000). Early paleoenvironmental investigations of these feedbacks focused on the positive boreal forest snow-masking feedback.

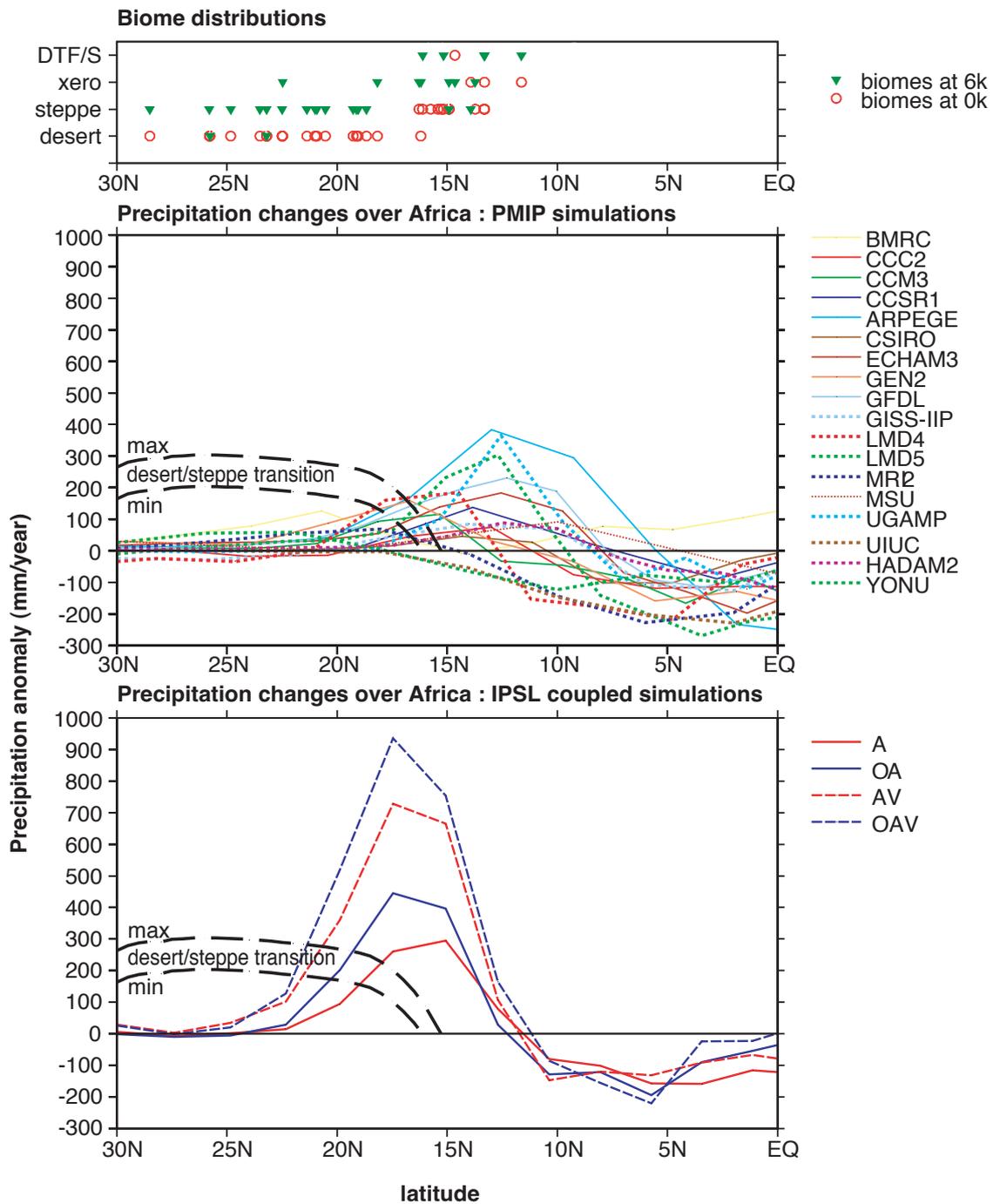


Fig. 5.3. Observed and simulated vegetation (top) and climate (precipitation, middle and bottom) change between 6000 yr B.P. and the present-day for northern Africa (20°W to 30°E) illustrating the importance of both ocean and vegetation feedbacks in estimating the correct sensitivity of the climate system to altered forcing (in this case astronomical forcing). Observations (top panel) indicate that the modern biomes (from north to south: steppe, xerophytic woodland/shrubland and tropical dry forest/savanna [DTF] shifted northward and displaced desert over much of North Africa in response to increased monsoon rainfall at 6000 yr B.P. Efforts to simulate these precipitation shifts using astronomical (Milankovitch) forcing alone (middle panel, no ocean or vegetation feedbacks, each line represents one of 18 atmospheric general circulation models) fail to generate the levels of precipitation increase (> 200 mm/year) needed to move the desert – steppe boundary as far north as indicated by the observations (Joussaume et al. 1999). In contrast, the addition (lower panel) of interactive ocean (OA), interactive vegetation (AV), and interactive ocean and vegetation (OAV) in a sequence of climate model experiments made with the same model (Braconnot et al. 1999) generates the simulation of incrementally greater precipitation. It is anticipated that more realistic ocean and land-surface feedbacks will eventually allow the northward expansion of steppe and wetter vegetation to be simulated correctly. Figure redrawn from Braconnot et al. 1999 and IPCC 2001.

However, subsequent work has illustrated that ocean feedbacks may have accounted for a large part (ca. 50%) of the circum-boreal region warming in the mid-Holocene that was previously ascribed to forest expansion and vegetation feedback alone (Figure 5.4; Hewitt and Mitchell 1998, Kerwin et al. 1999). These studies highlight the need to understand vegetation and ocean feedbacks more fully, and also how critical it is to tap the paleoenvironmental records of both climate forcing and response.

An understanding of vegetation feedbacks also should consider the influence of time-dependent patterns of vegetation change. Several studies have examined how land-use change may have altered regional to global climate change over the last several centuries. Chase et al. (2000) and Govindasamy et al. (2001) used the same land-cover change datasets, but different global climate models, and reached surprisingly different conclusions about the role of land-cover change in driving recent climate variations. These studies demonstrated that regional impacts were significant, yet even the direction of the change was difficult to estimate. One study (Chase et al. 2000) simulated virtually no net global temperature change, whereas the other experiment (Govindasamy et al. 2001) indicated that anthropogenic land-cover change was responsible for a significant amount (0.25°C) of global cooling over the last 1000 years (also in agreement with Brovkin et al. 1999). In yet another study, Claussen et al. (1999) showed how vegetation feedbacks may induce significant nonlinearities into the response of the climate system to gradual Milankovitch forcing.

The recent wealth of paleoenvironmental research on biophysical climate feedbacks is only the first step. We have yet to isolate the exact roles played by the terrestrial biosphere relative to competing influences, most notably ocean feedbacks. The next step is not only better climate system models, but also dynamic biosphere (e.g. vegetation) models that can simulate realistic responses of vegetation to changes in climate and atmospheric trace-gas concentrations. In addition, we need much improved observations of past environmental changes, including those of past vegetation, sea-surface state and aerosol levels (Kohfeld and Harrison 2000), all in the hope that we can improve our understanding of processes, while at the same time carrying out increasingly rigorous paleoenvironmentally-based evaluations of predictive models. The remainder of this synthesis focuses on what we know about the terrestrial biota's response to climate change, and thus what we must be able to simulate.

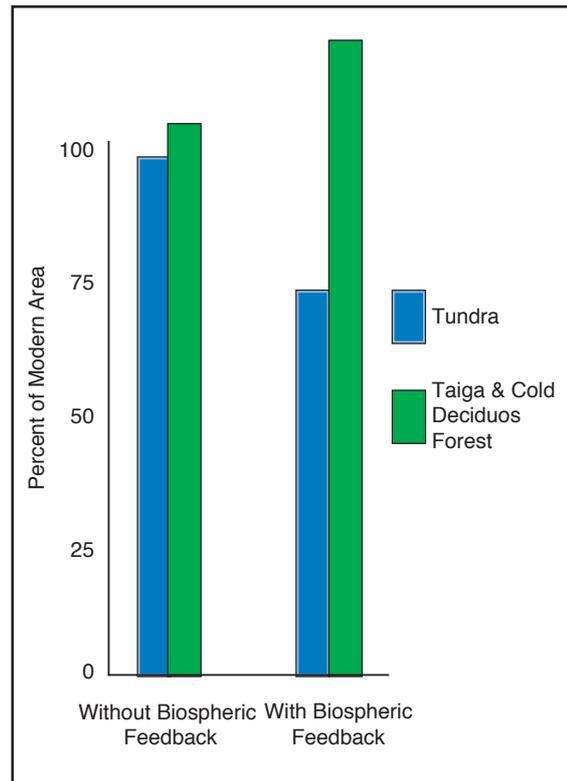


Fig. 5.4. Climate model simulations highlighting the importance of biosphere (e.g. albedo) feedbacks in estimating the correct temperature response (sensitivity) of the high northern latitudes to altered climate forcing. In this case (Foley et al. 1994; TEMPO Members, 1996), two identical climate model experiments were made, one with biospheric (albedo) feedbacks and one without. The experiment with the feedbacks generated 1.6°C greater warming at high latitudes on annual basis (>3°C in spring due to a greater snow masking effect), as well as a resulting greater northward movement of taiga and forest at the expense of tundra. This greater climate sensitivity and northward movement of biomes is in accord with paleoecological data, although more recent studies (Hewitt and Mitchell, 1998; Kerwin et al. 1999) suggest that ocean feedbacks may account for about half of the sensitivity ascribed to vegetation by TEMPO Members (1996).

5.3 Terrestrial biosphere changes in the past

Paleoecological and ecological studies reveal the hierarchy of effects of changing climate on the terrestrial biosphere that occur at different temporal, spatial and taxonomic scales. The consequences of high amplitude climatic change on Quaternary time scales are fundamentally different from those on shorter, ecological time scales over which the amplitude of climate change is relatively small. The nature of the biotic response to Quaternary climatic changes thus provides the best basis for understanding how ecosystems adjust in the face of substantial climate change. Such insights help define the envelope of natural biotic variability and serve

as a benchmark for assessing biotic responses to projected future climate changes.

5.3.1 Response of the biosphere

Our understanding of the past indicates that the biosphere responds to climatic variations in several ways:

Growth and/or death

There is an extensive literature focused on the response of individual plants and animals to climate variability, and the paleoenvironmental record provides key insights. Dendroclimatological studies provide long time series illustrating the strong role of temperature, moisture and other climatic variables in modulating plant growth (e.g. Cook and Cole 1991, Graumlich 1993a, Graumlich 1993b, Briffa et al. 1998, Cook et al. 1999, D'Arrigo et al. 1999, Hughes et al. 1999, Barber et al. 2000), as well as in driving tree mortality when environmental extremes exceed the ability of individuals to cope (e.g. Stine 1994, Arseneault and Payette 1997). More theoretical climate-growth relationships underlie whole classes of vegetation models (Botkin 1972, Solomon 1986), but the limited success of these models in simulating long records of past vegetation change indicates the complexity of climate-growth relationships. Moreover, dendroclimatological studies also illustrate how climate-growth relationships can change through time in as yet poorly understood ways (Briffa et al. 1998, Jacoby and D'Arrigo 1995).

Species migration

The ability of species to shift their geographic location in response to climate change, referred to as species migration, is perhaps one of the strongest patterns in the Quaternary record. Species ranges are limited by features of the macroclimate (such as growing-season warmth, winter cold, potential evapotranspiration), and these parameters define a unique "climate space" for each taxon. Migration in response to changes in the geographic location of suitable "climate", or "environmental" space (Bartlein et al. 1986, Austin et al. 1990, Webb et al. 1993, Jackson and Overpeck 2000) is most evident on continental and sub-continental scales, where networks of fossil sites reveal large-scale biogeographic adjustments during glacial-interglacial cycles (Figure 5.5; Bernabo and Webb 1977, Webb 1981, Huntley and Birks 1983, Delcourt and Delcourt 1987, Huntley 1988, Webb 1988, Birks 1989, Prentice et al. 1991). Rapid range shifts have also been documented at smaller spatial and shorter temporal scales in response to abrupt climate changes (Ritchie and MacDonald 1986, Gear and Huntley 1991). Species migration has been best

documented for higher plants, because of the abundance of well-dated pollen sites, but the fossil records of mammals, molluscs, and insects show comparable responses (Elias 1994, FAUNMAP Working Group 1996, Ashworth 1997, Preece 1997).

The biogeographic changes evident in the last 21 kyr required rates of migration that would be considered unprecedented in modern times. For example, tree taxa in eastern North America and Europe moved at a rate of 200-1500 m/yr in response to climatic warming at the end of the last glaciation (Davis 1976, Huntley 1988, Webb 1988, Birks 1989). These rates are observed today only in the case of exotic species invasions, which are often assisted by human activities. Like the spread of weeds, rare long-distance dispersal events leading to the establishment of small, remote populations, followed by a quiescent phase of little discernible range change, and an active phase of explosive expansion were probably important components of Quaternary migrations (Pitelka and the Plant Migration Workshop Group 1997, Clark et al. 1998).

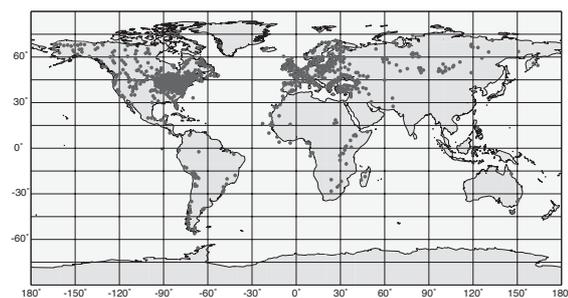


Fig. 5.5. An important component of our increased knowledge of terrestrial biosphere dynamics over the last decade has stemmed from the explosion of public-domain paleoclimatic and paleoecological data available at the World Data Center for Paleoclimatology, Boulder: www.ngdc.noaa.gov/paleo/paleo.html. The map shows distribution of 1551 sites with fossil pollen data that are available globally. Other extensive paleobiological data holdings exist at the WDC, including thousands of sites in tree-ring and faunal databases, and hundreds of sites in plant macrofossil and insect databases. Collaborating data efforts of many scientists in many countries have been key to the success of PAGES data activities.

Changes in community composition

Because individual organisms adjust to climate forcing independently, the composition and structure of biotic communities can change substantially. On glacial-interglacial time scales, communities have been subjected to wholesale reorganizations in composition as a result of species migration (Huntley and Webb 1988). In the course of such movement, the arrival of new species and the loss of others altered communities at particular locations. On shorter time scales, regional climate variations,

often occurring abruptly, affected the composition and structure of communities by altering the natural disturbance regime and existing competitive interactions (e.g. Tinner and Lotter 2001). The paleoecological record indicates that communities can undergo dramatic changes in a matter of decades to centuries. These changes involve species movements, and thus represent individualistic responses to climate change, but the spatial scale of the change is limited. For example, drought events in this century have caused sufficient tree mortality to cause an expansion of steppe at the expense of forest in the American Southwest (Swetnam and Betancourt 1998). Similarly, deciduous forest and wooded steppe replaced steppe in southern Europe in less than two centuries in response to climate variations within the last glacial period (Allen et al. 1999, Allen et al. 2000). The movement of species was not great because areas of suitable climate space remained within the immediate topographically complex area.

Changes through evolution

Little macroevolution is evident within the Quaternary, probably because of the rapid nature of environmental fluctuations relative to species lifespans (Bennett 1990, Bennett 1997). Nonetheless, morphological variations in some groups suggest that Quaternary climate change has resulted in continual selection for favorable ecotypes (Cronin 1985, Smith et al. 1995, Rousseau 1997, Davis and Shaw 2001). For example, morphological variation in fossil molluscs is evident throughout the Quaternary, although even extreme fossil morphotypes are found within the range of present-day forms (Rousseau 1997). Current genetic and morphological variation within western North American conifer species is also attributed to protracted periods of allopatry (geographic separation) during glacial periods, although isolation was apparently not long enough for speciation to occur (Critchfield 1984). Some groups of mammals (including humans) have also undergone substantial morphological change in the last 2 million years (Lister 1993).

Extinction

The total loss of a species can result from an inability to migrate or adapt to environmental change. Extinction may occur with the loss of suitable environmental conditions, or else the loss of spatial or temporal contiguity of such conditions (Figure 5.6; Huntley 1999). Environmental change may also reduce or fragment a species range to the extent that population(s) lack the genetic variability to survive natural perturbations, such as extreme climatic events, an epidemic pathogen outbreak, or a wild-

fire. Species existing at the margin of suitable conditions are also rendered more susceptible to multiple stresses, such as human hunting, in the face of climate change.

The geologic record is punctuated by episodes of mass extinction as a result of rapid, sometimes catastrophic environmental change (Raup and Sepkoski 1984, Eldredge 1999, Kring 2000). The most recent prehistoric extinction event occurred in the late Pleistocene, when many large-bodied vertebrates (Stuart 1993, Lister and Sher 1995, Sher 1997), and at least one tree species (Jackson and Weng 1999), became extinct during the last glacial termination. At that time many other species were extirpated from parts of their overall range; for example, *Ovibos moschatus* (musk ox) was extirpated from Eurasia, although it persisted in the North American Arctic. Although human hunting pressures likely contributed to late-Pleistocene megafaunal extinctions (Alroy 1999, Martin and Steadman 1999), vertebrate populations were also stressed by environment changes imposed as a result of rapid global warming (Graham and Lundelius 1984, Graham and Mead 1987). Their failure to adjust to changing environments did not arise from the magnitude of the climate change alone, because other glacial terminations of the same general character were not accompanied by major extinction events. It is more likely that the rapid rate of environmental change at the end of the last glaciation led to spatial and temporal discontinuities in required environmental conditions. Landscape fragmentation and climate change in North America and South America, for example, coupled with the presence of human hunters, proved fatal.

The ability to adjust to environmental changes of different rates and magnitudes is a necessary strategy for species persistence. However, the capacity of the terrestrial biosphere to keep pace with climate change has varied across temporal scales (Prentice 1986, Webb 1986, Prentice 1992, Webb and Bartlein 1992, Webb et al. 1998). For example, short-term fluctuations in climate have often invoked little or no responses, especially in long-lived organisms. Intermediate rates of climate change have caused a complex nonequilibrium response, in which some parts of the system respond immediately and others lag behind. Slow variations in climate solicited a time-dependent equilibrium response. On millennial and longer time scales, the terrestrial biosphere has been in dynamic equilibrium with climate, and variations in the biosphere directly and indirectly contributed to changes in the climate system. On shorter time scales, lags in the response of organisms and ecosystems have led to periods of disequilibrium. The magnitude of the

disequilibrium depends on the rate and location of changing potential range and the intrinsic characteristics of the taxa to migrate or adapt. Complex responses may arise from non-linear interactions occurring at different temporal scales. For example, gradual changes in climate may result in radical shifts in the equilibrium state (Ritchie and MacDonald 1986). In addition, more than one equilibrium state may occur because of feedbacks within the ecosystem. For example, the response to natural disturbance, such as fire events, can result in a variety of stable states in the vegetation, depending on the intensity and duration of the disturbance and the legacy of recent history. Consequently, changing climates may yield several outcomes in the response of the biosphere.

Spatial scales are also an important consideration in assessing biosphere response. At the global and hemispheric scale, large patterns in vegetation physiognomy are subject to climatic constraints, as evidenced by the fact that the distribution of biomes can be predicted by equilibrium models that assume a direct control by climate (Prentice et al. 1992, Haxeltine and Prentice 1996). Changes in vegetation at the global scale affect changes in total carbon storage in vegetation, peats, and soils, and these carbon pools are an important component of the climate system. At the regional scale, species have been shown to be in equilibrium with climate during some parts of the Quaternary and out of phase at other times. Thus, they are more limited by their intrinsic capacities at some times than at others. Vegetation changes at this scale have altered regional climate by changing evapotranspiration rates and albedo properties (Foley 1994, Kutzbach et al. 1996, Claussen and Gayler 1997, Broström et al. 1998, Farrera et al. 1999). At the landscape and local scales, biota may require a few hundred years to respond to climate change or the appearance of new species (Solomon et al. 1981, Davis and Botkin 1985, Overpeck et al. 1990).

5.3.2 The temporal hierarchy of climate change and biospheric response

The causes of prehistoric climate and biosphere variations are often described as hierarchical ranging from those operating at a global scale over millennia to those occurring at the local scale over seasons to decades (Table 5.1, Mitchell 1976, Delcourt et al. 1983, Bartlein 1988, Prentice 1992, Webb and Bartlein 1992).

The “tectonic” frequency band (>1 million years)

On the longest and largest scales are climate variations resulting from changes in the distribution of land, sea, and mountain ranges, as well as long-term

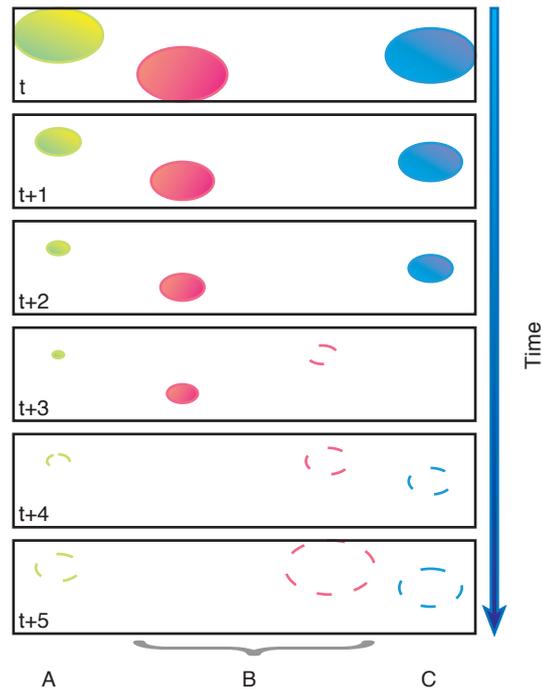


Fig. 5.6. Three alternative extinction mechanisms are illustrated by the sequence of panels. Time advances from the top panel downwards, as indicated by the arrow. As time advances the climate of the geographical area represented by the rectangle changes progressively. This climate change impacts upon the location and/or extent of the geographical area within which each species' climatic requirements/tolerances are met. These areas are represented by the ellipses that are shaded if the species is occupying them and empty with a dashed outline if the species is absent. Species A (green) experiences a progressive and severe reduction in its potential range from time t to time $t+3$, followed by an increase at times $t+4$ and $t+5$. The extreme reduction of its range at time $t+3$, however, renders it extremely susceptible to stochastic extinction as a consequence of extreme environmental events or random population fluctuations; thus it has become extinct before the subsequent increase in its potential range at time $t+4$. Species B (red) experiences progressive but less severe range reduction from time t to time $t+3$. However, at time $t+3$ a second discrete area of potential range becomes available in a different part of the overall geographical space. By time $t+4$ the original component of the potential range has disappeared; the new component, however, has increased in extent and does so again at time $t+5$. The species nonetheless becomes extinct because it is unable to achieve the long-distance dispersal necessary to cross the spatial discontinuity between the two component parts of its potential range at time $t+3$. Species C (blue) experiences a progressive but moderate range reduction from time t to time $t+2$. At time $t+3$, however, no part of the geographical space offers climatic conditions that satisfy its requirements/tolerances and it thus has no potential range. Although suitable conditions are once again available at time $t+4$ and the area of its potential range increases once again thereafter, it has become extinct at time $t+3$ as a consequence of the temporal discontinuity in its potential range.

changes in the earth's energy balance due to changes in atmospheric composition (Ruddiman and William 1997, Zachos et al. 2001). These occur in the “tectonic” (or geologic) frequency band.

Table 5.1. Response of biota to climate variations on different time scales

FREQUENCY BAND	SCALE OF VARIATION (YEARS)	KIND OF VARIATIONS	CAUSES	CHARACTERISTIC BIOTIC RESPONSES
Tectonic	>10 ⁶	Cenozoic cooling onset of glaciation	Tectonics, continental drift, atmosphere evolution	Creation of new biomes, speciation, major extinction events
Orbital	10,000-1,000,000	Glacial- interglacial cycles	Seasonal cycle of insolation and trace gases, tectonics	Repeated formation and breakup of biomes, some extinction and speciation, selection at subspecies level
Millennial	1000- 10,000	Multi-millennial variations in climate within a glacial period	Ice sheets, insolation, trace gases, regional ocean-atmosphere dynamics	Species migration at the regional to continental scale, community reorganization, selection at the subspecies level
Interdecadal-Centennial	10-100	Decadal to centennial climate variations	Internal variations in the climate system, solar variability, impact of volcanic eruptions	Changes in community composition and structure through recruitment, mortality and natural succession
Annual-Interannual	<10	Storms, droughts, ENSO events	Internal variations in the climate system, solar variability, volcanic eruptions	Adjustments in physiology, life history strategy, and natural succession following disturbance

Climate variations on this long frequency band are responsible for the cooling trend in the late Cenozoic, as well as the onset of northern hemisphere glaciation about 2.5 million years ago (Maslin et al. 1998). Such changes, directly or indirectly, led to major extinction and speciation events, as well as the first appearance of new biomes, including deserts, grasslands, and tundra (Verba et al. 1995, Davis and Moutoux 1998). Tectonic-scale climate changes have also been tied to the evolution of ecosystems and hominids in Africa (De Menocal 1995).

The “Orbital” frequency band (1 million to 10,000 years)

On glacial-interglacial time scales, or the “orbital” (Milankovitch) frequency band, climate change is attributed to variations in earth-sun orbital relations and their influence on insolation at different latitudes and during different seasons (Berger and Loutre 1991). In the Quaternary, the superposition of variations in the timing of perihelion with 19 and 23 ka periods, obliquity with a 41 ka period, and eccentricity with a 100 ka period has produced a sequence of changes in the latitudinal and seasonal

distribution of insolation that are the “pacemaker of the ice ages”. These variations resulted in changes in the size of continental ice sheets, ocean temperature and circulation, and atmospheric composition that constitute glacial/interglacial oscillations (Figures 5.1 and 5.7; Imbrie et al. 1993; Chapter 3, section 3.1). In terms of biotic responses, orbital variations on glacial-interglacial time scales resulted in repeated formation and break-up of biomes, including the appearance and disappearance of tropical rainforests, boreal forest, tundra and deserts (Huntley and Webb 1988, Overpeck et al. 1992, Markgraf et al. 1995, Colinvaux et al. 2000, Jackson et al. 2000, Jackson and Overpeck 2000, van der Hammen and Hooghiemstra 2000). Species responded individually in “dynamic equilibrium” with environmental forcing (Webb 1986, Prentice et al. 1991). Species migrations and biome shifts created opportunities for specialization of taxa and the elimination of less-fit or rare species through extinction. The biotic changes have resulted in continual genetic reshuffling as species ranges become alternately continuous and fragmented. Speciation events are rare in the Quaternary (Bennett 1997), probably because the direction of environmental change has been reversed over

time scales too short for directional adaptive evolutionary responses to have played any significant role.

Biotic responses on orbital time frequencies are evident in long pollen records from different parts of the world (De Beaulieu and Reille 1984, De Beaulieu and Reille 1992, Reille and De Beaulieu 1995, Watts et al. 1996, Whitlock and Bartlein 1997, Davis 1989, Davis and Moutoux 1998, Allen et al. 1999, Allen et al. 2000, Whitlock et al. 2000). These records show shifts in vegetation types that match well changes in the seasonal cycle of insolation, global ice sheet size, and more regional changes in the ocean-climate system (Figure 5.7). Periods when orbital variations were different from those of the last 21 kyr resulted in vegetation assemblages with no late-Pleistocene or Holocene analogs. The close correspondence between changes in vegetation and variations in insolation and ice-sheet volume confirm that climate is the primary driver of regional vegetation change on these time scales.

Networks of paleoecological sites are available for the last 21 kyr and can be used to examine the spatial patterns of biotic change at orbital band frequencies within an interglacial period (World Data Center-A for Paleoclimatology: Global Pollen and Plant Macrofossils Databases). Because a primary Northern Hemisphere and tropical biotic response to these variations was species migration (Figure 5.8; see also Huntley 1988, Webb 1988, Prentice et al. 1991, Elias 1994, FAUNMAP Working Group 1996, Jackson et al. 2000, Webb et al. 1998), com-

munities appear ephemeral, continually being formed and dismantled. Assemblages with no modern counterpart were particularly common prior to the Holocene when the combination of a large ice sheet, low summer insolation, cool sea-surface temperatures, and low greenhouse gases created unique climatic conditions in particular regions (Figure 5.8; Prentice et al. 1991, Overpeck et al. 1992, Williams et al. 2001). In contrast, the primary biotic response at higher latitudes in Southern Hemisphere was more a shrinking and re-expansion of biomes rather than differential species migration (Markgraf et al. 1995); climate change does not always result in climate or vegetation without modern analogs.

In mountainous areas, shifts in biogeographic range on orbital time scales were less dramatic, because areas of suitable conditions were available locally, often simply at a different altitude (Barnosky 1987, Thompson 1988, McGlone et al. 1993, McGlone 1997). Suitable microclimates to sustain populations during unfavorable periods, and sufficient habitat connectivity to allow population expansion during amelioration, have allowed montane species to respond rapidly to climate change (Figure 5.9). Allen et al. (1999) note that future warming could drive populations off the top of mountains, and hence overwhelm the natural resiliency of mountain environments. This history of repeated fragmentation and connection has led to considerable subspecific variation within extant montane taxa. This type of selection for favorable ecotypes is one consequence of climate changes on orbital frequency bands.

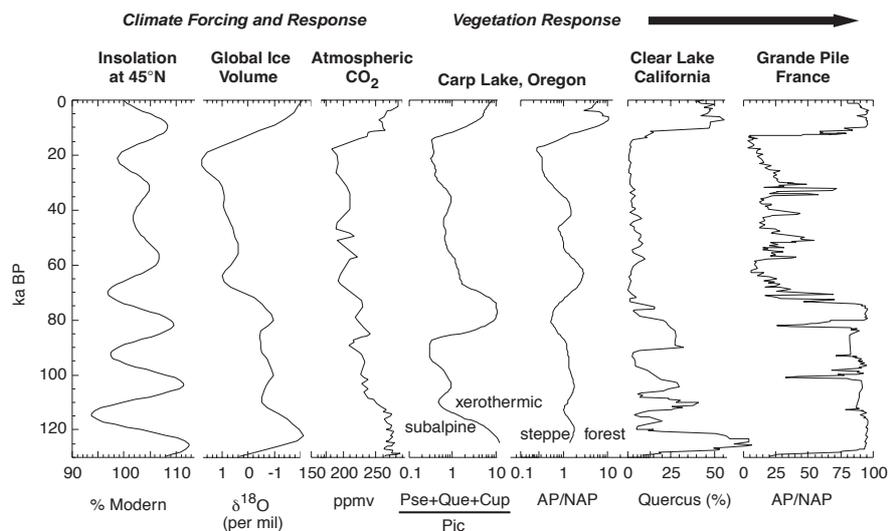


Fig. 5.7. Time series of climate forcing and large-scale climate response and vegetation change at two sites in North America (Carp and Clear Lakes, in Oregon and Northern California respectively) and Europe (Grand Pile, France). See Figure 1 for sources of insolation, ice volume and atmospheric CO_2 concentration data. The ratios of the sum of *Pseudotsuga-Larix* (Pse), *Quercus* (Que) and Cupressaceae (Cup) pollen percentages to *Picea* (Pic) pollen percentages, and of total arboreal pollen (AP) to nonarboreal pollen (NAP) provide an indication of vegetation type and openness at Carp Lake (Whitlock et al. 2000). *Quercus* pollen percentages at Clear Lake (Adam 1998).

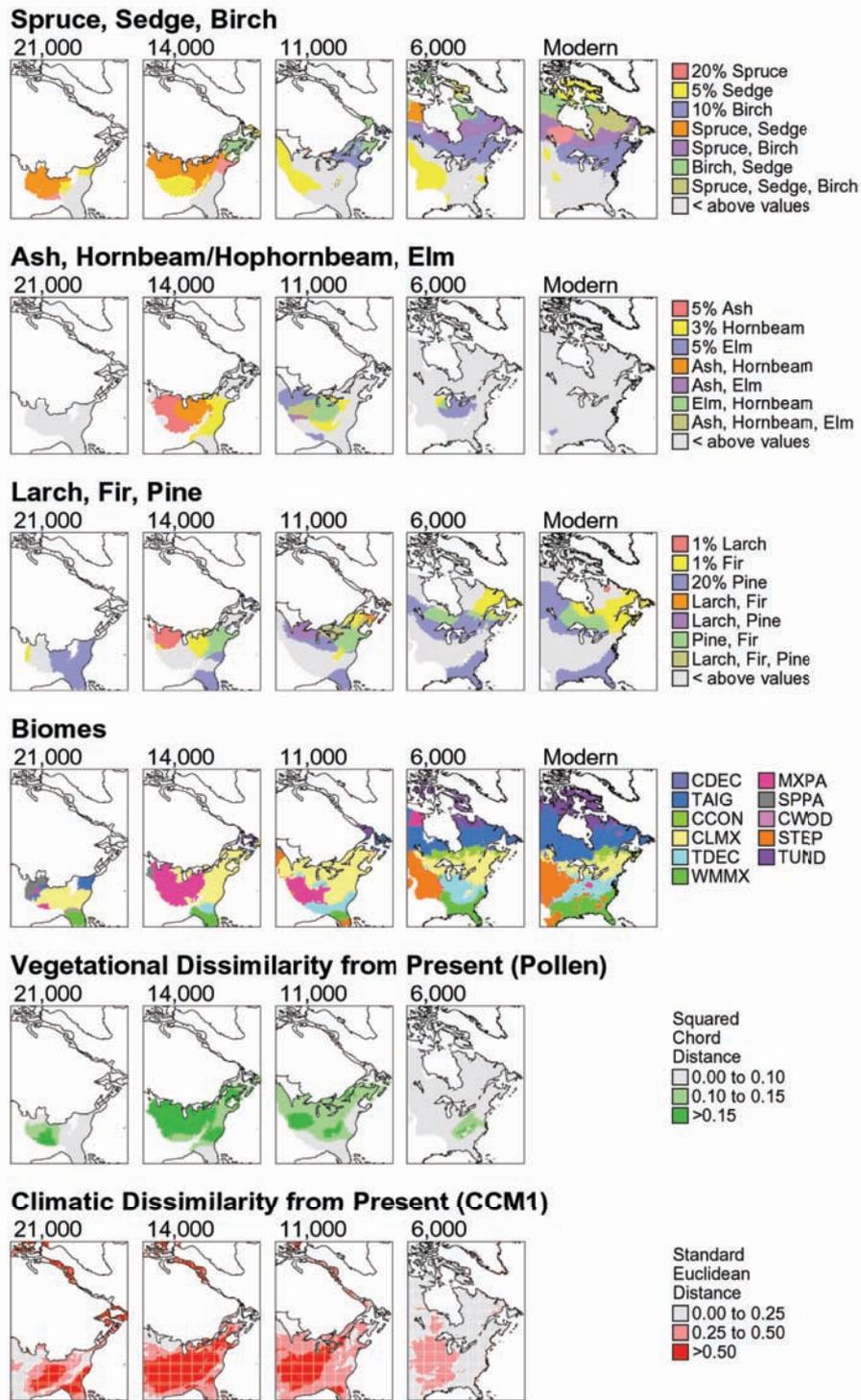


Fig. 5.8. Vegetation change and climate forcing over the last 21,000 years in eastern North America based on the analysis of 490 fossil pollen records and climate model results (after Williams et al. 2001). Late-Pleistocene and modern plant associations mapped (white areas = no data or ice sheet) as multi-taxon isopolls (top three rows, after Jacobson et al. 1987) and biomes. Differences in color between maps indicate a change in plant associations. Biome maps were created using the affinity score technique (Prentice et al. 1996) and the biome definitions of Williams et al. (2001), with spruce parkland and mixed parkland added to represent late-Pleistocene plant associations (Cold deciduous forest CDEC, Taiga TAIG, Cool Conifer forest CCON, Cool Mixed Forest CLMX, Temperate Deciduous Forest TDEC, Warm Mixed Forest WMMX, Mixed Parkland MXPA, Spruce Parkland SPPA, Conifer Woodland CWOD, Steppe STEP and Tundra TUND). The bottom two rows indicate the dissimilarity of the fossil pollen samples or climate simulations from their most similar modern counterpart.

The millennial frequency band (10,000 to 1,000 years)

On shorter time scales, climate changes in the millennial frequency band include abrupt shifts in ocean-atmosphere-cryosphere (Fig 5.9; Chapter 3, section 3.2). Millennial-scale climate changes, including so-called Dansgaard-Oeschger (D-O) cycles, and Heinrich (H) events, are best known from marine and ice-core records from the North Atlantic region and Europe (Chapter 3). Heinrich event H0, the Younger Dryas (11.6-12.9 cal ka; Alley et al. 1993), is registered clearly in ice-core and ocean records in the North Atlantic and pollen data from Europe (e.g. Watts et al. 1996, Litt et al. 2001); and it is also described for other parts of the world (e.g. Hu et al. 1995, Peteet 1995). Evidence of anomalous conditions (not always cold and dry) corresponding with H1, H2, H3, and, in some cases, H4 through H6, is reported in Europe (e.g. Figure 5.9; Watts et al. 1996, Allen et al. 1999, Allen et al. 2000), eastern North America (Grimm et al. 1993), and the western U.S. (Benson et al. 1996, Benson et al. 1998, Hicock et al. 1999, Whitlock and Grigg 1999, Grigg et al. 2001). Although first described in Marine Isotope Stage (MIS) 2 and 3 (Bond et al. 1993), millennial-scale variations in climate have also been recorded in the Holocene, previous interglacials and early Pleistocene (Overpeck 1987, Bond et al. 1997, Raymo et al. 1998, Bond et al. 1999, Oppo et al. 2001). The ultimate cause of this millennial-scale variability is still not completely understood (Chapter 3), but it is responsible for changes in the strength and location of atmospheric features, and it accounts for some of the variations in climate and vegetation history on centennial to millennial time scales (Figure 5.9; Grimm et al. 1993, Watts et al. 1996, Allen et al. 1999, Whitlock and Grigg 1999, Allen et al. 2000, Tinner and Lotter 2001). The biotic response on these time scales includes regional shifts in species distributions and changes in the composition of plant communities (Figure 5.9). Heinrich events in southern North America, for example, shifted vegetation composition in both Florida (cool/dry versus warm/wet during H events) and Missouri (opposite phasing) (Grimm et al. 1993, Dorale et al. 1998, Grimm 2001) and D-O events in southern Europe caused alternations of forest and steppe (Allen et al. 1999). The rapid response on the part of forest taxa probably was accomplished by selection of cold and warm ecotypes within nearby species pools.

Sub-millennial frequency bands (<1000 years)

Changes in climate occurring on time scales of centuries or less are ascribed to changes in volcanic activity, atmospheric greenhouse gas concentra-

tions, solar output, and internal climate system dynamics (Rind and Overpeck 1993, Robertson et al. 2001; Chapter 3, section 3.3 and Chapter 6, section 6.10). Such changes are best documented in high-resolution records, including tree-rings, ice cores, lake sediments and corals (Overpeck et al. 1997, Mann et al. 1999, Briffa 2000, Crowley and Lowery 2000, Gagan et al. 2000, Urban et al. 2000, Jones et al. 2001). Likewise, variations at the inter-annual time scale, such as individual droughts, have been identified in the paleoclimate records where annually resolved records are available (Laird et al. 1996, Cole and Cook 1998, Stahle et al. 1998a, Stahle et al. 1998b, Woodhouse and Overpeck 1998, Touchan et al. 1999). At sub-regional scales, short-term climate fluctuations, including ENSO-related variations, helped to shape disturbance regimes and landscape-level vegetation patterns. Climatic extremes on these time scales have been responsible for dramatic changes in species mortality and recruitment patterns at the local to regional scale (Payette et al. 1996, Swetnam et al. 1999). In addition, ENSO-type variations play a role in life-history strategies that influence the pattern of reproduction and growth in particular species (Swetnam and Betancourt 1998, Finney et al. 2000).

5.3.3 The roles of changing disturbance regimes and atmospheric CO₂

Disturbance as an agent of change

Natural disturbances, such as fire, wind storms, disease, and extreme climatic events, are important triggers of rapid biotic response that can serve to reduce the response time to a given climatic change, and also to alter the composition of affected ecosystems (Davis and Botkin 1985, Overpeck et al. 1990, Clark et al. 1996, Swetnam and Betancourt 1998, Camill and Clark 2000). Long fire records suggest that many major vegetational changes during the Quaternary were associated with shifts in the fire regime (Bird and Cali 1998, Long et al. 1998, Tinner et al. 1999, Carcaillet and Richard 2000, Clark et al. 2001). On millennial time scales, variations in fire regime are attributed to climate changes caused by variations in the seasonal cycle of insolation, even in areas where the vegetation did not change (Millsbaugh et al. 2000). At centennial and shorter time scales, climate/weather, vegetation composition, and ignition frequency all shape the fire regime, because vegetation determines fuel availability, and fires, in turn, create landscape patterns that influence vegetation recovery (Bergeron and Archambault 1993, Swetnam 1993, Clark et al. 2001). Changes in disturbance regime

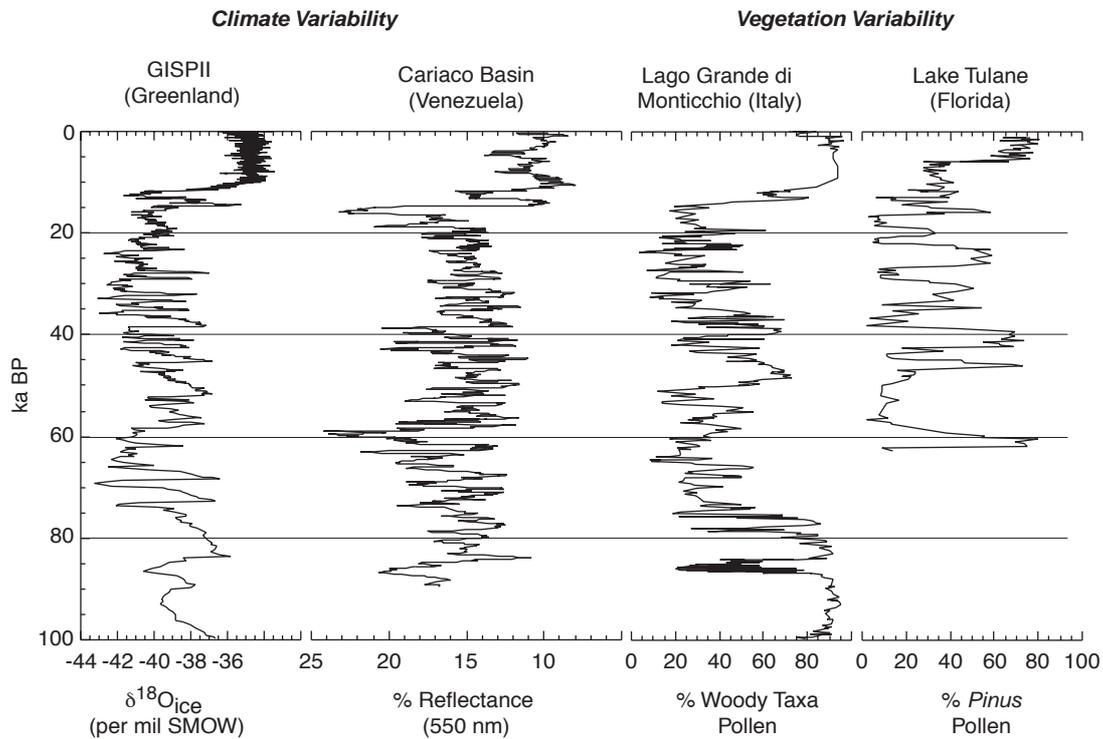


Fig. 5.9. Time series of millennial-scale climate variability in the circum-North Atlantic region (Peterson et al. 2000, Stuiver and Grootes 2000) and reconstructed vegetation variability for sites in eastern North America (Grimm et al. 1993) updated by (Grimm 2001) and Europe (Allen et al. 1999).

shift the competitive balance within communities, favoring species that are better adapted to the new conditions. It also creates opportunities for new species to invade and colonize, as evidenced by the role of fire in the migration of spruce across Scandinavia (Bradshaw and Zackrisson 1990, Bradshaw and Hannon 1992).

The direct effects of changing atmospheric CO₂ concentrations

Changing concentrations of atmospheric CO₂ have the potential to affect the biosphere directly, just as they do indirectly through climate change. Altered atmospheric CO₂ has the potential to influence plant growth optima, canopy density, stomatal conductance, and water-use efficiency, and apparently did so at the Last Glacial Maximum (LGM – 21,000 yr B.P.), when CO₂ levels fell to about 200 ppmv (Solomon and Shugart 1984, Jolly and Haxeltine 1997, Street-Perrott et al. 1997, Collatz et al. 1998, Cowling 1999, Cowling and Sykes 1999, Levis and Foley 1999, Cowling et al. 2001, Huang et al. 2001). Indeed, it has been suggested that the ~200ppmv minimum seen in ice cores during glacial times represents a limit

that reflects reduced photosynthetic efficiency, below which the global biosphere is restricted in its ability to further lower atmospheric CO₂ levels (Falkowski et al. 2000). The direct impacts of lowered CO₂ at the LGM are hard to detect, however, highlighting the primacy of climate in driving much of the observed shifts in species and biome ranges. It is likely that LGM forest cover was more open (Cowling 1999, Farrera et al. 1999, Levis and Foley 1999, Cowling et al. 2001), and C4 species (e.g. grasses) were able to expand into many areas at the expense of C3 species as a result of the lower CO₂ levels (Collatz et al. 1998, Huang et al. 2001). Moreover, the biophysical impacts of these CO₂-driven changes on LGM climate may have been significant (Collatz et al. 1998, Cowling 1999).

5.4 Terrestrial biosphere change of the future: out of the envelope and into a world of disequilibrium

5.4.1 Future climate change

The latest assessment of future climate change (IPCC 2001) suggests that projected increases in

greenhouse gases in the atmosphere will likely transform the climate in many regions beyond the historic envelope of variability observed in the last million years (Figs. 5.1 and 5.2). Even if global temperature changes by the end of the 21st century are at the low end of the current IPCC estimated range (1.4 to 5.8°C), the magnitude and direction of regional climate changes (e.g. in temperature and available moisture) could be without precedent in recent earth history, particularly when coupled with the large changes in atmospheric composition that will drive the climate change. Global and, in many cases, local rates of climate change are also likely to exceed any seen in the last million or more years (Figure 5.2), especially if the sensitivity of the climate system to doubled atmospheric trace gas concentrations is closer to the upper end of the estimated IPCC range. Lastly, there is no reason to believe that global warming will cease at the end of this century. Even if levels of atmospheric trace gases are stabilized, the earth's climate system will continue to react for thousands of years as a result of feedbacks among the oceans, atmosphere, cryosphere and biosphere. Longer term impacts will include continued sea-level rise and continued slow warming (IPCC 2001).

5.4.2 Future biosphere change

The simplest assessments of the possible future state of the terrestrial biosphere are based on simulations of the equilibrium response of vegetation to some new atmospheric composition, for example a doubled atmospheric concentration of CO₂ (Figure 5.10). Such simulations have been made both for global vegetation, in terms of the extent and distributions of major units (biomes) (e.g. Woodward et al. 1998, Sykes et al. 1999); and for individual species at a variety of geographic scales from that of Great Britain (Hill et al. 1999), to that of North America (Solomon 1986, Overpeck et al. 1991, Bartlein et al. 1997, Shafer et al. 2001), and Europe (Huntley 1995, Huntley et al. 1995, Sykes et al. 1996, Sykes 1997, Hill et al. in press).

The key points to emerge from the equilibrium biome simulations are: first, simulations of past climate that do not incorporate terrestrial biospheric feedbacks underestimate important components of the climate response. Second, even without incorporation of these feedbacks, the climate simulated for the future is likely to result in substantial changes in the extent and location of biomes on the earth's surface, as well as in major shifts in the location of ecotones that are involved in important feedbacks (e.g., the forest-tundra

ecotone in northern Eurasia).

The potential for large ecosystem changes is further emphasized by simulated future climate-induced shifts in individual species ranges. The potential ranges of important tree species in North America (e.g. Shafer et al. 2001 and Figure 5.11) illustrate the magnitude of future biotic responses at the regional scale. They also emphasize (Figure 5.12; Bartlein et al. 1997) that in areas of topographic complexity, such as the western USA, the biogeographic response is not always simple poleward or upslope displacements. Although projected suitable conditions for some taxa are indeed located north of, or at higher elevations than, their present range, for other taxa they are found to the south or in the same general location (Bartlein et al. 1997). Such a wide range of possible responses becomes particularly critical for conservation strategies that aim to conserve biodiversity (i.e. threatened and endangered species) in the face of climate change.

Future changes in species ranges are not restricted to plants (Figure 5.13). Just as invertebrates and vertebrates exhibited large spatial responses to past climate changes (Graham 1992, FAUNMAP Working Group 1996, Ashworth 1997, Graham 1997, Preece 1997), large changes in animal distributions will be required to maintain equilibrium with projected future climate changes. Indeed, the paleoecological record, as well as model projections, suggest that species at all trophic levels are capable of large-scale biogeographic shifts in response to climate change, either directly or via climate-induced changes in their habitat.

5.4.3 The need to focus on the transient response

A major limitation of the simulations discussed above (section 4.2) is that they are portrayals of potential future equilibrium states that may never be realized, or at best, are likely to be achieved only following a substantial lag during which disequilibrium will prevail. The high probability of such lags arises principally from the unprecedented rate and large magnitude of predicted future climate changes (Figure 5.2). The most rapid recent global warming of large magnitude occurred at the last deglaciation. The transition from fully glacial to fully interglacial conditions spanned at least nine millennia (15,000 to 6,000 years ago) and represented a global warming of at least ca. 5°C (Webb et al. 1997, Pinot et al. 1999); this equates to an average rate of ~0.06°C per century, although warming was faster during parts

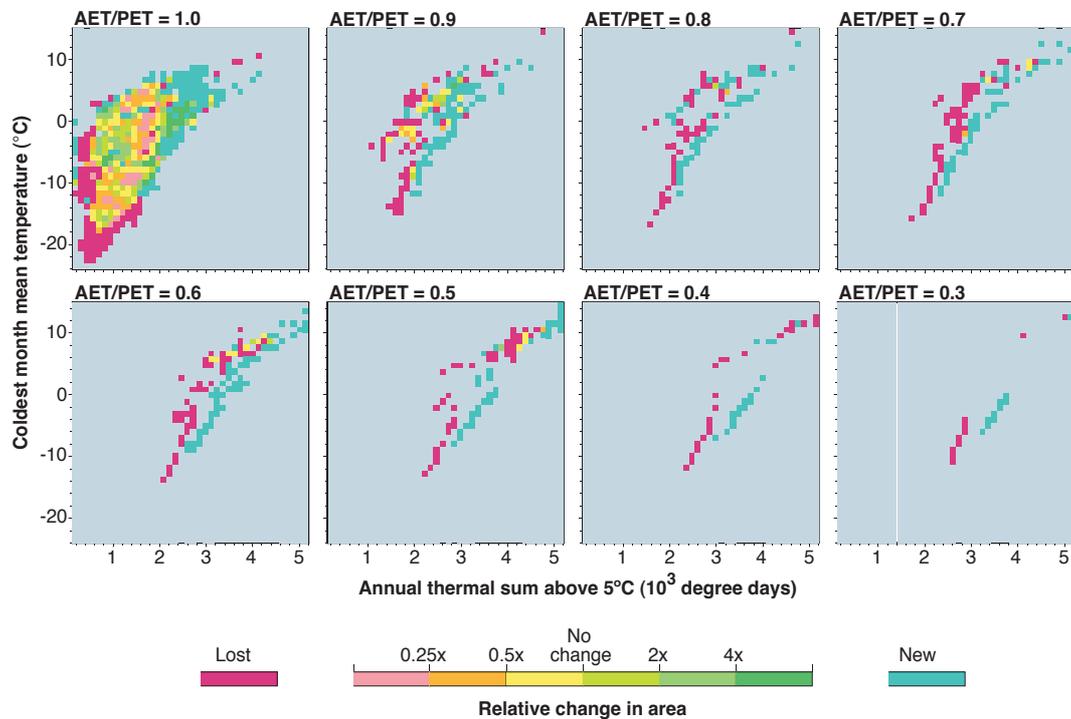


Fig. 5.10. Example illustrating potential shift in European multivariate climate space by the end of the 21st century given modest global warming (2.8°C). In this example, the multivariate climate space is defined by three key bioclimatic variables (coldest month mean temperature, annual thermal sum above 5°C, and water stress defined as the ratio of actual to potential evapotranspiration [AET/PET]). The changed climate scenario is derived from the climate simulated for a doubling of CO₂ by a global climate model (Schlesinger and Zhao 1989) close to the low end (2.8°C global mean warming for a doubling of atmospheric CO₂) of the IPCC (2001) range. Given continued present levels of greenhouse gas emissions, bioclimate will change dramatically throughout Europe by the end of the century, with large areas experiencing conditions without a present analog ('new') and many present combinations of conditions no longer represented ('lost'). Such changes will force substantial, although difficult to predict, changes in the terrestrial biosphere of the region.

of the deglaciation. In contrast, the most conservative estimates of future warming suggest that the global mean temperature will rise by ca. 1.5°C within the next century — a rate many times faster than during the deglacial transition. Both the paleoecological evidence (Davis 1976, Huntley 1991) and studies of recent species' range expansions (Thomas 1991, Hill et al. 1999) indicate that the maximum rates at which most species can expand their ranges are between 200 and 2000myr⁻¹. The principal exceptions to such rates are exotic ruderals (species characterized by a short life cycle, rapid population growth and widely dispersed propagule (e.g. *Bromus tectorum*, cheatgrass, Mack 1981) or highly mobile vertebrates (e.g. muskrat and collared dove; Van den Bosch et al. 1992), which can spread even faster. Thus, most but not all, plant species will be unable to maintain equilibrium with the potential range shifts seen, for example, in Figure 5.13. If shifts of up to 1000 km are re-

quired to maintain equilibrium with the climate change simulated for the next century, as projected for Europe by the HADCM2 GCM (Mitchell et al. 1995), species ranges there would have to change at rates of up to 10 km yr⁻¹ — five times faster than the fastest rates in the past, and as much as 50 times faster than the rates achieved by many species.

Although it might be argued that some past climatic fluctuations, for example Dansgaard–Oeschger cycles, occurred at similarly rapid rates, these changes were of relatively modest global magnitude, and were soon reversed. Future warming is likely to be of relatively large global magnitude, unidirectional, and will continue for at least several centuries and/or to an eventual equilibrium with an atmospheric CO₂ several times the pre-industrial level or more (IPCC 2001). The lack of any modern or Quaternary analog insofar as climate is concerned suggests that species' ranges will significantly lag future climate changes and

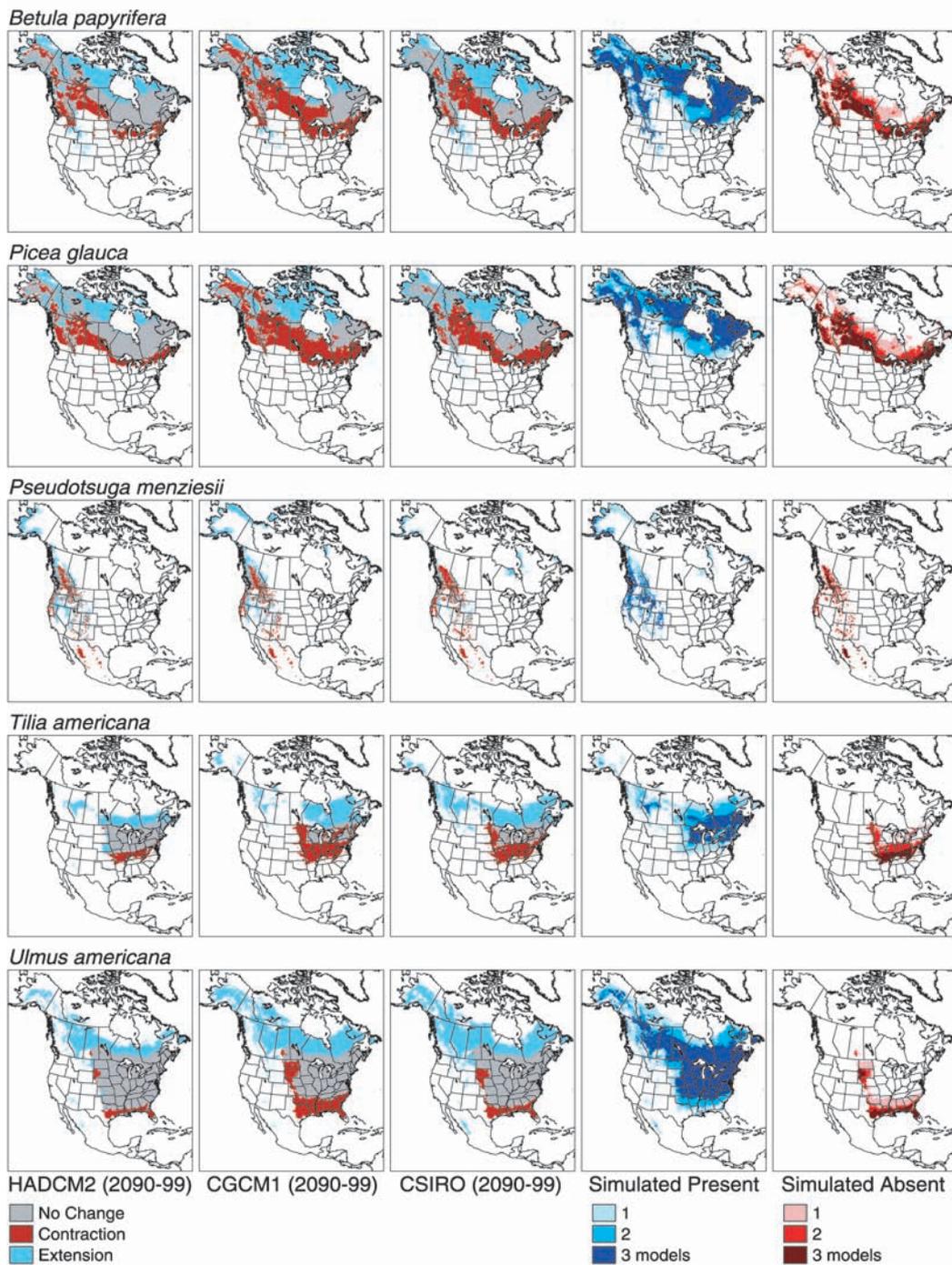


Fig. 5.11. Comparison of observed distributions with future simulated distributions for fire tree species in North America using climate scenarios for 2090-2099 generated by three climate change simulations HADCM2, CGCM1, and CSIRO GCMs (Shafer et al. 2001, left three columns). "No change" indicates where the species is observed at present and is simulated to occur under future climate conditions; "contraction" indicates where the species is observed at present but is simulated to be absent under future climate conditions; and "extension" indicates where the species is not observed at present but is simulated to occur under future climate conditions. Agreement among the future distributions of each species as simulated by the three GCM scenarios is displayed by showing for each grid point the number of models that simulate a species to be present or absent (right two columns). Figure from Shafer et al. (2001).

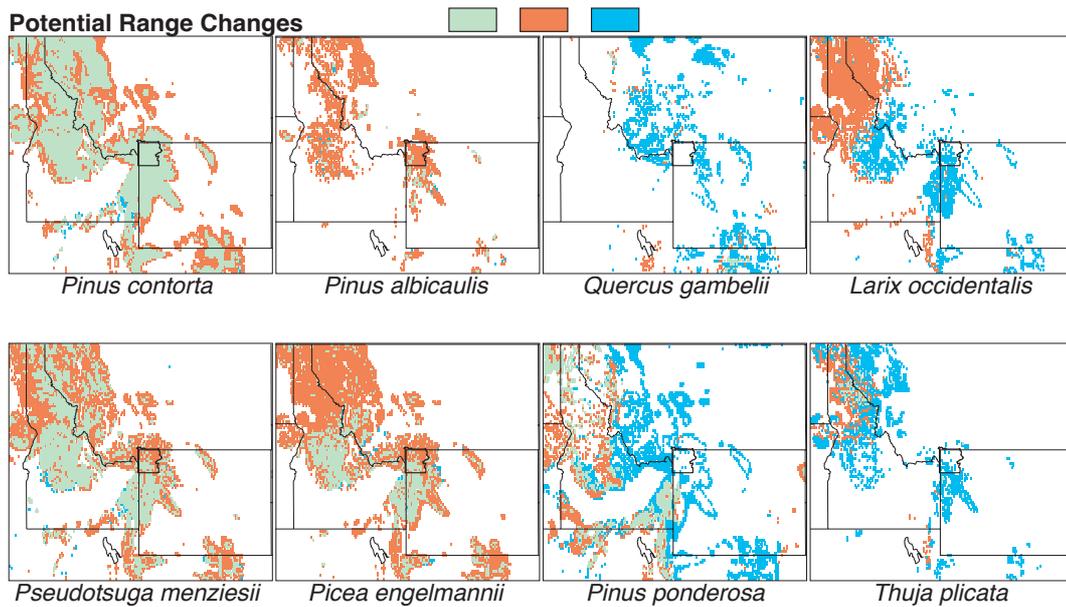


Fig. 5.12. Potential range changes for selected tree taxa in Yellowstone National Park under one global warming scenario. Green shading indicates grid points where a specific taxon occurs under both the present and 2xCO₂ climate, red shading indicates grid points where a taxon occurs under the present climate, but does not occur under 2xCO₂ climate, and blue shading indicates grid points where a taxon does not occur under the present climate, but does occur under the 2xCO₂ climate. Figure from Bartlein et al. (1997).

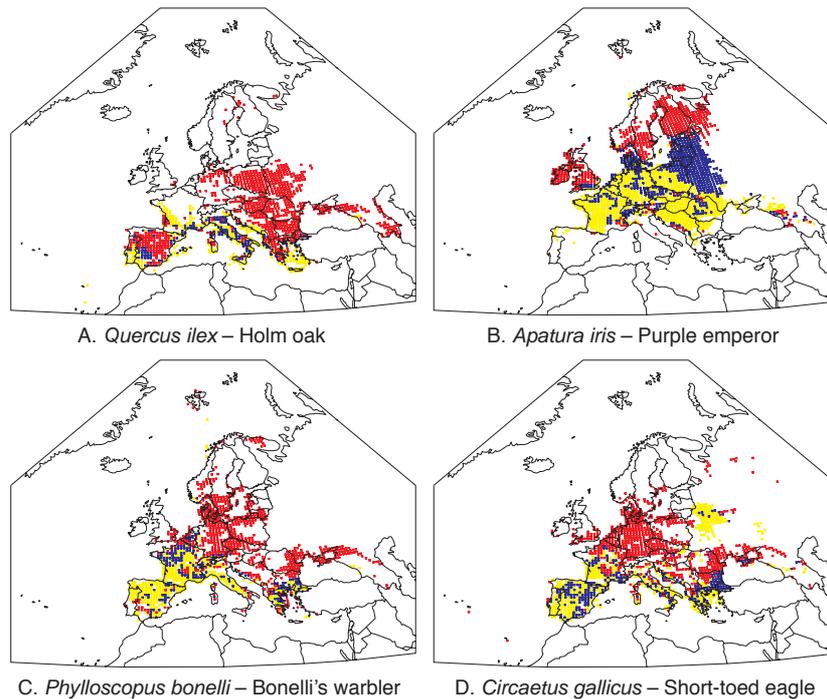


Fig. 5.13. The potential ranges of the species were simulated using a scenario derived from the last 30 years (2070–99) of the HADCM2 transient simulation using both greenhouse gases and sulphate aerosol forcing (Mitchell et al. 1995) applied to climate response surfaces fitted to the species' recorded European ranges and the climate corresponding to the period from which the records were derived (1931–60 from Leemans and Cramer (1991) for *Quercus ilex* and 1961–90 from New et al. (1999) for the remainder). As in previous studies (Hill et al. 1999; Huntley et al. 1995), three bioclimate variables were used to fit the response surfaces (coldest month mean temperature, annual temperature sum above 5°C, and an estimate of the ratio of actual to potential evapotranspiration). The data used to derive the models relate to a 50 km UTM grid. The models for all four species fitted well, as assessed using the kappa statistic (Monserud and Leemans 1992) $0.70 \leq \kappa < 0.85$ – 'very good' fit; $\kappa > 0.85$ – 'excellent' fit. The maps portray the present and potential future ranges

(Fig. 5.13. continued)

as simulated by the response surface model for each species. Blue dots signify grid cells simulated as potentially occupied under both the present and future climate; yellow dots indicate grid cells simulated as potentially occupied only for the present climate; red dots indicate grid cells simulated as potentially occupied under the future climate. The four species illustrated represent four trophic levels and are typical of many others that have been studied. **A.** *Quercus ilex* – Holm oak: an evergreen tree of southern and southwestern Europe ($\kappa = 0.78$) (distribution from Jalas and Suominen 1976). **B.** *Apatura iris* – Purple emperor: a widespread woodland butterfly whose larvae feed upon several *Salix* spp. (willows) ($\kappa = 0.87$) (distribution from Talman (1998) with the distribution used to fit the model truncated at 30°E because of the unreliability of the data from Russia). **C.** *Phylloscopus bonelli* – Bonelli's warbler: small insectivorous woodland bird of western and southwestern Europe ($\kappa = 0.78$) (breeding distribution from Hagemelijer and Blair 1997). **D.** *Circaetus gallicus* – Short-toed eagle: large raptor of partially-forested landscapes in southern Europe where it feeds primarily upon reptiles ($\kappa = 0.70$) (breeding distribution from Hagemelijer and Blair 1997).

possibly never achieve equilibrium with the new conditions because of their no-analog character.

Even with strenuous measures to reduce global trace-gas emissions, the future global warming driven by emissions to date is likely to be at least 1.5°C (IPCC 2001). As illustrated earlier (section 4.2), this warming alone will call for substantial range displacements by many species. Given the fragmentation of many species' habitats in the modern landscape, as well as the reduction in extent of available habitat, it is unlikely that many species will attain the migration rates observed during the late Quaternary (Overpeck et al. 1991, Bartlein et al. 1997, Collingham and Huntley 2000). In such circumstances, even a 1.5°C global mean temperature rise over the next century is likely to result in severe disequilibrium of the biosphere, with even the potentially most rapid migrants failing to adapt to climate changes. Were the climate change to cease at this level, centuries of stable conditions would likely then be required for many species and ecosystems to regain equilibrium with their environment.

Predicting the likely dynamic response of species is rendered more difficult by uncertainties about future disturbance regimes. Not only are the dynamic responses of species to climate change constrained by their dispersal abilities and by habitat availability, disturbance of the established vegetation is in many cases a prerequisite for the establishment of seedlings and hence for migration (Sykes and Prentice 1996, Pitelka and the Plant Migration Workshop Group 1997). Such disturbance may include changes in fire regime, pathogen outbreaks, and extreme climatic events, such as droughts, frosts or windstorms (Overpeck et al. 1990). Predicting future climate variability and extreme events is an area of current research in the climate modeling community, and the paleoenvironmental record can be used to help evaluate the performance of these models. However, predicting future “natural” disturbances will be more difficult than reconstructing past ones, as will be predicting future human disturbances.

5.4.4 More complicating factors

The foregoing sections make it clear that generating

accurate model-based assessments of future biotic responses to climate change is not yet possible. It is thus not possible to obtain accurate assessments of how future changes in the terrestrial biosphere will feed back on the rest of the climate system, both in terms of biogeochemistry and biophysics. This line of reasoning also means that it will be difficult to anticipate future threats to biodiversity and ecosystem dynamics, even if we could know future climate change with perfect accuracy.

Even with the paleoenvironmental record as a guide, it is difficult to project the response of the terrestrial biosphere to future changes at all spatial and temporal scales. Hemispheric- to continental-scale climate predictions are available but are too generalized to be of use in regional or local assessments. Future average surface-air temperature is perhaps the easiest to estimate, whereas biosphere-relevant changes in the distribution and availability of moisture, the frequency of extreme weather events and natural and human-induced disturbances are difficult to predict, especially at the local-to-regional scales where societal impacts are greatest.

The paleoenvironmental record is rich with examples of “surprise” climate system behavior (Broecker 1987, Overpeck 1996, Overpeck and Webb 2000, National Research Council 2002; Chapter 3). Dansgaard-Oeschger and Heinrich events, for example, provide us with examples of abrupt climate system behavior. It is also clear that abrupt shifts in hydrologic variability (e.g. the frequency, amplitude and duration of droughts or floods) have occurred and could thus continue to occur, particularly if the mean state of the climate system is changing rapidly in response to elevated atmospheric greenhouse gas concentrations. Making accurate assessments of future biospheric change is simply not possible given the possibility of future “surprise” climate changes.

Although it is possible to use paleoenvironmental and 20th century records of biotic and environmental change to describe the environmental conditions required by plant and animal species, this knowledge may be of limited use in assessing future changes in many regions given the projected magnitude. Because future climate forcings are unprecedented, many local climates will be unique

(Crowley 1990, Webb 1992). Atmospheric composition will also be unlike that seen by any of the extant species or ecosystems. Disturbance regimes may be unlike those seen before, particularly in the face of growing anthropogenic impacts (e.g. Balmford et al. 2001). In addition, land-use, invasive species, pollution, surface-water use, groundwater depletion, and altered predation will add to the uniqueness of future earth environments. Unfortunately, the rich records of the 20th century and the millennia before, are unlikely to reveal all that is needed to make accurate assessments of future biosphere change.

5.5 Conclusions and future research needs

The paleoenvironmental record has provided invaluable estimates of past climate change (both rates and magnitudes, from local to global scales), as well as indications of how the terrestrial biosphere responded to those changes (Davis 1989, Davis 1990, Huntley 1991, Davis and Shaw 2001). Comparisons of these past changes with those projected for the next century reveal that the rate, magnitude and destination of future climate change in many regions lie beyond the historical range of variability. As a consequence, the pressures placed upon the terrestrial biosphere by these changes also will be unprecedented.

5.5.1 The problem with biosphere feedbacks and climate sensitivity

Anthropogenic greenhouse gas emissions have already committed the world to a mean global temperature increase of at least 1°C by the end of the 21st century (IPCC 2001). However, if emissions continue at current rates, atmospheric CO₂ will double pre-industrial levels before the end of the century, and cause mean global warming to at least 1.4°C, and perhaps significantly more (IPCC 2001). The paleoclimatic evidence discussed above, moreover, suggests that poorly constrained biospheric and oceanic feedbacks may limit the ability of state-of-the-art climate models to estimate the full sensitivity of the climate system to altered forcing. Future regional temperature and precipitation changes could thus be larger than presently anticipated. True regional climatic changes, especially at high latitudes where feedbacks are strongly positive, may be large, non-linear, and inherently difficult to project. In turn, these uncertainties render it difficult to make regional assessments of terrestrial biosphere change with any degree of certainty. Poorly constrained biospheric feedbacks

also result in major uncertainties with respect to other important parts of the earth's climate system. For example, even the relatively modest (~1°C or less) global warming during the last interglacial period led to substantially reduced ice volumes and corresponding increases in sea level of 5-6 m relative to present (Cuffey and Marshall 2000, Lambeck and Chappell 2001). Ice melting and sea level rises were even more substantial during earlier interglacials. These past changes suggest that climate sensitivity, or the magnitude of climatic response to a given (i.e., trace-gas) forcing, may indeed be larger than previously estimated.

5.5.2 Implications for future biodiversity conservation

The established global network of national parks and nature reserves is a key part of our global ecosystem and biodiversity conservation strategies. However, the future climatic conditions in many parks and reserves (e.g. Yellowstone Park, Bartlein et al. 1997) will differ substantially from those prevailing in the same locations today, and, as a result, the nature of the ecological communities in these parks and reserves is likely to change substantially. Consequently, parks and reserves may fail to protect the species and ecosystems they were set up to protect.

Yellowstone Park (Figure 5.12) is far from unique, and approximately half the world's protected areas are likely to experience climate-driven change of an extant biome (Leemans and Halpin 1992). Many such changes would result in almost complete species turnover, and hence likely threaten the rare or endangered species they were designed to protect. Moreover, many of the world's biodiversity hotspots (Myers et al. 2000) are also vulnerable to wholesale shifts in environment caused by abrupt climate change and projected sea level rise (Figure 5.14).

More generally, loss of biodiversity, particularly with respect to late-successional species, can be predicted as a consequence of the widespread disequilibrium between the terrestrial biosphere and climate. Ruderal species are likely to be the beneficiaries of this disequilibrium. Introduced species will also benefit and become even more widespread. One outcome of this climate-induced change is thus likely to be a tendency for communities to become dominated by early-successional and non-native species, and for vegetation to become increasingly homogeneous over broad geographical areas. Both at regional and global scales, biodiversity loss will occur principally among late-successional species characterized by Grime (1978)

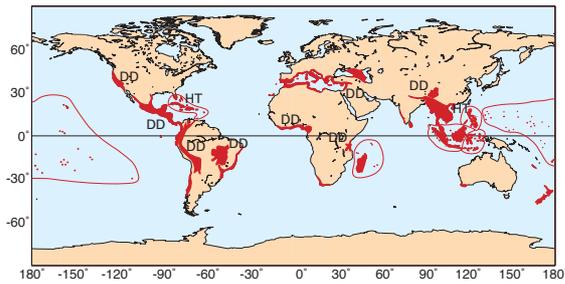


Fig. 5.14. Annotated map of biodiversity hotspots (after Myers et al. 2000) indicating those that are in regions known to have experienced decadal “megadrought” (DD – Cross et al. 2000; Heim et al. 1997, Hodell et al. 1995, Ledru et al. 1998, Maley and Brenac 1998, Morrill et al. in press, Salgado-Labouriau et al. 1998, Sifeddine et al. 2001, Stine 1994, Verschuren et al. 2000) or abrupt shifts in tropical storm (i.e. hurricane or typhoon) landfall frequency (HT – Liu and Fearn 1993, Liu and Fearn 2000, Liu et al. 2001) in the past. Note that hotspots without annotation may also be susceptible to abrupt climate shifts, but detailed paleoclimatic data are lacking from these areas.

as ‘stress-tolerators’ (Thompson 1994). Projected climate changes also pose a substantial risk to genetic diversity (Huntley 1999, Davis and Shaw 2001). During the inevitable phase of climate-biosphere disequilibrium, species may occupy only a small fraction of their overall potential climatic range. If, as is often found to be the case, species exhibit genetically-determined clinal variation that is continuous in space in relation to major climatic variables (e.g. Mooney and Billings 1961), then the reduced population is likely to retain only a small part of the species overall genetic flexibility to climatic variation (Figure 5.15). Even if the climate subsequently stabilizes and the species has the opportunity to re-occupy the whole of its former potential climatic range, it may be unable to do so due to a loss in its former genetic variability.

The foregoing example serves to illustrate both one of the principal consequences of biodiversity loss – a loss of potential adaptability of the terrestrial biosphere to changed conditions – and also perhaps the principal value of biodiversity. Biodiversity at the species level, as well as at the level of intra-specific genetic diversity, renders the terrestrial biosphere adaptable to changing environments (Lawton 1999). Species that may, under one set of conditions, be relatively rare and/or play only a minor role in the biosphere, may under changed conditions become dominant (McGlone et al. 1993, McGlone 1997). Although rare species thus may appear “redundant” in relation to biospheric function under present conditions, they are better viewed in the same way as so-called “redundant systems” in an engineering context – they play a vital role when the species currently providing major biospheric functions are, as a result of changed conditions, no longer able to provide those

functions.

Given the importance of biodiversity for the future adaptability of the biosphere, and hence of its preservation, the potential problems faced by many species in the future must be addressed. A comparison with the paleoecological records indicates that many species ranges will be unable to immediately adjust to future climate change. It may thus be necessary to consider assisted migration or translocations of some species as part of an overall conservation strategy. In other cases, it may be necessary to plan to diversify landscapes and to incorporate more patches (and reserves) of wildlife habitat in order to facilitate species’ migration through highly modified agricultural/urban landscapes (Huntley 1999). Deliberate manipulations of the disturbance regime may also be required in cases where species’ migration is hindered by their inability to establish in a currently prevailing community; this is likely to be especially important in the case of many forest species and ecosystems.

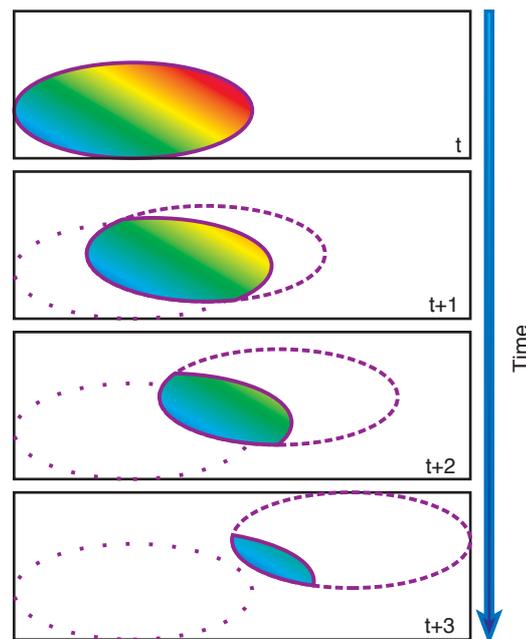


Fig. 5.15. Potential loss of genetic diversity as a consequence of rapid climatic change. Each rectangular panel represents the same geographical space, the four panels representing successive steps along a timeseries of climatic change that advances downwards, as indicated by the arrow. The ellipse in each panel represents the climatically determined potential range of the species in that geographical area at that time. As a consequence of climatic change the species’ potential range shifts north-eastwards with time. The shaded area in each panel indicates the area where the species is present at that time step, i.e., its realized range. At time t the species fully occupies its potential climatically-determined range, as indicated by the shading of the entire ellipse. Thereafter the area occupied by the species progressively diminishes in size through time, because the rate at which the species’ population is able to migrate is less than the rate required to maintain equilibrium with the rapidly changing

(Fig. 5.15. continued)

climate, whereas the species is unable to persist in areas of its former range that are no longer climatically suitable. The species' realized range thus becomes progressively more restricted to the southwestern part of its potential range. The spectrum of shading across the species' realized ranges represents clinal adaptive genetic variation in some character(s) related to the principal climatic gradient spanned by the species' realized range at time t . It is assumed that gene flow through the species' population is sufficiently rapid that there is no lag in gene 'migration' relative to the rapid climatic change. At time t the full range of genotypes (from red to blue) is present along the climatic gradient across the species' realized range. As the realized geographic range decreases in extent, however, it also decreases with respect to its range along the climatic gradient with respect to which the species exhibits clinal variation. Thus at time step $t+1$ the species no longer occupies that part of the climatic gradient to which the red genotypes are adapted, with the result that they are lost from the population. By time step $t+3$ only genotypes close to the blue extreme of the cline are able to persist within the species' realised geographic range. The extent to which such loss of diversity may be irreversible depends upon the underlying genetics; if alleles associated with the red genotype are not maintained in populations at the opposite end of the cline then the loss will be effectively irreversible. It should be noted that, were gene 'migration' to lag climate as much as does the migration of the species' population, then the genotypes able to occupy the 'realized range' at time $t+3$ previously would have become extinct, and with them the species as a whole.

5.5.3 Principal uncertainties and research imperatives

Both the paleoenvironmental and biosphere dynamics research communities have accomplished a great deal over the last 10-15 years, but they have only set the stage in terms of gaining a predictive understanding of future climate and biosphere change. The importance of biosphere-climate feedbacks has been demonstrated, and the next decade needs to be devoted to quantifying the exact nature of these feedbacks through extensive monitoring, process-based studies, and earth-system modeling. In the next ten years, the focus in paleoclimate-biosphere research should include more focus on transient and site-specific responses, and how well these responses are simulated with predictive models. This shift in emphasis will be critical for assessing future climate changes, including the biogeochemical, biogeographic, ecosystem, and biodiversity consequences at regional and finer scales. At these spatial scales, the impacts of other stresses (e.g. disturbance, nutrients, atmospheric chemistry, pollution, land-use, and other human influences) will also have to be explicitly considered.

Assessments of future conditions without a strong paleoenvironmental component will not be successful. As made clear in this chapter, the centuries- to millennia-long records of past climate and biosphere change are the only information we have on the nature and consequences of large environmental changes. Future paleoenvironmental research

should improve our understanding of climate variability, as well as biospheric responses and feedbacks. It should also include an emphasis on high-resolution records that disclose the nature of inter-annual to century-scale climate and biosphere change, with a focus on short-term, as well as long-term responses of the biosphere to climate variability and change. Lastly, there should be more investigations that examine the ecological consequences of future climate change in a context of what actually happened in the past. This will provide much needed reality checks for simulations and assessments of future change, and will be most successful if carried out with greater interaction among disciplines that have traditionally worked in isolation, most notably the paleoenvironmental, ecological and land-use management, climate and climate modeling, and social science communities.

5.5.4 The final word

Meeting the research challenges in the preceding section will yield the understanding required to make realistic predictions of future regional climate and biosphere change, but probably only if future climate changes are at the low end of the IPCC 2001 range (<1-2°C; IPCC 2001). Paleoenvironmental observations and research will thus be a key component of what is needed. Gaining a much improved predictive understanding, coupled with improved strategies for the conservation of genetic, species and ecosystem biodiversity (e.g. redundant reserves, enhanced migration mechanisms, and control of non-climatic stresses) could help avert a major mass extinction.

However, a larger climate change (> ca. 1-2°C/century), or a lack of improved conservation strategies, will likely make a mass extinction inevitable. As this synthesis makes clear, it will probably be impossible to predict how regional climates, ecosystems and populations will be affected by changes in atmospheric composition and climate that are unprecedented, particularly when these changes are coupled with other anthropogenic stresses such as pollution, land-use, invasive species, predation, alteration to disturbance regimes, depletion of ground water, diversion of surface water, and elimination of migration routes and mechanisms. The inherent inability to predict how the biosphere will respond to future climate change also precludes accurate assessments of the biosphere's role in influencing future biogeochemical cycles (e.g. atmospheric composition) and climate. Because these influences are likely to be significant on regional scales, the likelihood of accurate regional climate predictions will also be further

diminished.

The possibility of abrupt climate change also reduces the odds that extinctions can be avoided, unless new conservation strategies are implemented explicitly to reduce vulnerability to abrupt change. For example, many types of abrupt changes (e.g. widespread sustained drought, or shifts in the size and frequency of tropical cyclones) are, at present, not predictable. Anticipated large changes in climate forcing also increase the possibility that an unfavorable abrupt shift in climate variability could be triggered without warning (National Research Council 2002). Paleoenvironmental research is at the heart of understanding the dynamics of abrupt climate change, and should also be central to understanding how the terrestrial biosphere responds to abrupt climate change.

However, just as the large and rapid climate change, coupled with human hunting activity, proved disastrous to large animals over the last deglaciation, the combined stresses of climate change and human activity could create an unprecedented ecological disaster. Given that it is entirely possible that a doubling of atmospheric CO₂ could drive a global temperature increase of 2°C or more, as well as larger regional changes (IPCC 2001), there is only one way to ensure that

we do not trigger a mass extinction. First, we must limit future greenhouse-gas emissions to the atmosphere, and second, we must adopt a more sophisticated global conservation strategy that acknowledges the threats of climate change in the face of multiple additional anthropogenic stresses.

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