# Climate Change

T he Earth's climate is vastly different now from what it was 100 mil-
lion years ago when dinosaurs roamed the planet and tropical plants
thrived closer to the poles. It is different from what it was 20,000 years
ago when ice sheets covered much of the Northern Hemisphere. Although
the Earth's climate will surely continue to change, climatic changes in the
distant past were driven by natural causes, such as variations in the
Earth's orbit or the carbon dioxide (CO_2) content of the atmosphere.
Future climatic changes, however, will probably have another source as
well—human activities. Humans cannot directly rival the power of natur-
al forces driving the climate—for example, the immense energy input to
the Earth from the sun that powers the climate. We can, however, indi-
rectly alter the natural flows of energy enough to create significant cli-
matic changes. The best-known way people could inadvertently modify
climate is by enhancing the natural capacity of the atmosphere to trap
radiant heat near the Earth's surface—the so-called greenhouse effect.
This natural phenomenon allows solar energy to reach the Earth's surface
and warm the climate. Gases such as water vapor and CO_2, however, trap
a much larger fraction of long wavelength radiant energy called terrestri-
al infrared radiation near the Earth's surface. This causes the natural
greenhouse effect to be responsible for some 33°C (60°F) of surface
warming. Thus, seemingly small human-induced changes to the natural
greenhouse effect are typically projected to result in a global warming of
1°C to 5°C in the next century (Intergovernmental Panel on Climate
Change 1990, 1996a). This could result in an ecologically significant
change, which is why climatic considerations are fundamental in the dis-
cussion of the status and trends of ecological conditions.

We may already be feeling the climatic effects of having polluted the
atmosphere with gases such as CO_2. Many activities associated with
human economic development have changed our physical and chemical
environment in ways that modify natural resources. When these
changes—such as burning fossil fuels that release CO_2 or using land for
agriculture or urbanization that cause deforestation—become large
enough, significant global (worldwide) changes are expected. Such mod-
ifications can disturb the natural flows of energy in Earth systems and
thus can force climatic changes. These disturbances are also known as
global change forcings. Quantitative evaluations of the potential effect of
human activities in creating global change are needed. Such evaluations
are also central to potential policy responses to mitigate global changes
(Schneider 1990; Intergovernmental Panel on Climate Change 1996b,c).

How can human societies prepare for so uncertain a climatic future?
The ability to predict that future with a known degree of confidence
would help. The processes that make up a planet's climate, however, are
too large and complex to be reproduced physically in a laboratory.
Fortunately, they can be simulated mathematically with the help of com-
puters. In other words, one can devise mathematical expressions for the
observed behavior and the physical principles that govern the system—
laws of thermodynamics and Newton's laws of motion. The computer can
then calculate how the climate would change (Trenberth 1992). For rea-
sons detailed in this chapter, mathematical climate models cannot simu-
late the full complexity of reality, but they can, in combination with field
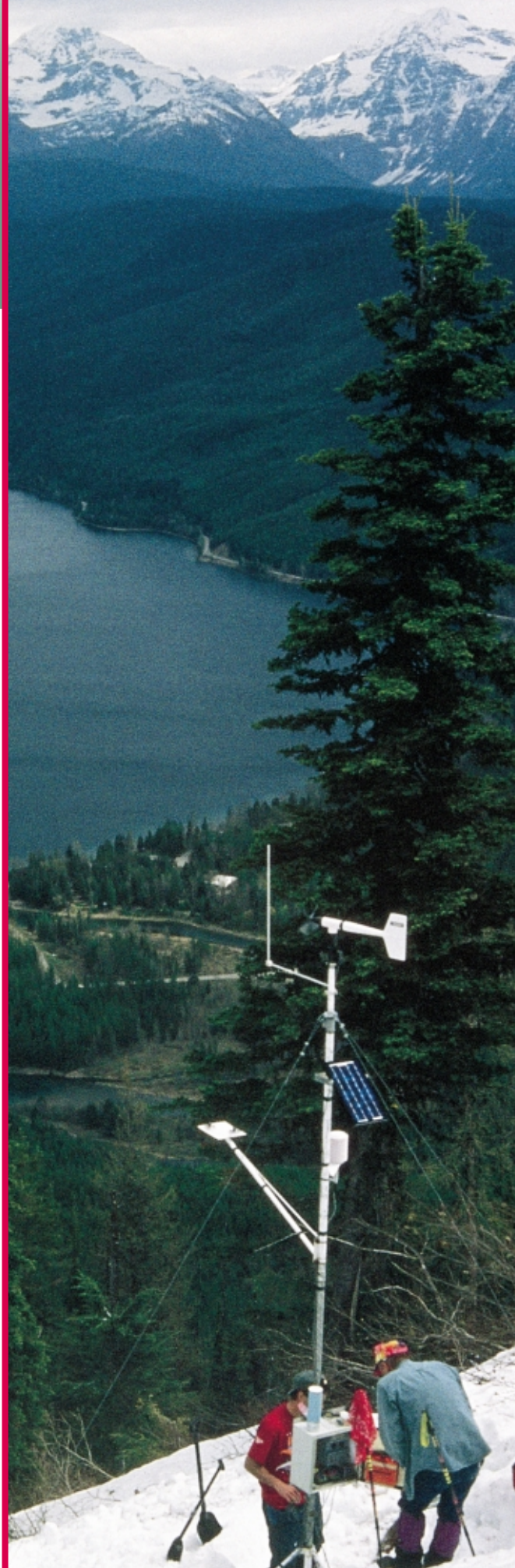
Courtesy Glacier National Park archives

and laboratory studies, reveal important aspects of how the climatic system operates. The critical scientific tasks are to formulate, build, and verify the models to produce ecologically useful forecasts. Verifying these forecasts requires knowledge of how the actual climate has changed.

What Has Happened

About 2.5 million years ago, continents moved into roughly their present positions. Antarctica was, by then, completely covered with an ice sheet, and year-round sea ice developed in the Arctic Ocean. Although permanent polar ice has been present since then, the polar ice caps and other ice masses have expanded and contracted on a 40,000-year cycle. About 750,000 years ago, this cycle was joined by a much longer (100,000-year) and more intense cycle of ice ages and relatively ice-free periods (interglacials). For example, an ice age occurred about 150,000 years ago and an interglacial from about 140,000 to 120,000 years ago; the last major glacial ice age peaked about 20,000 years ago, and the current 10,000-year-long interglacial period (Holocene) began (Lorius et al. 1990; Fig. 1). Scientists can reconstruct these events because when snow falls on high, cold glaciers two notable aspects are preserved: the air trapped between snow grains is eventually transformed into air bubbles as the snow is compressed into ice from the weight of subsequent accumulations, and the ratio of two oxygen molecules with different molecular weights (O^{16} and O^{18} isotopes) is a proxy record for the temperature conditions that existed when the snow was deposited. Cores taken from holes drilled into some 2,000 meters of ice on Greenland and Antarctica show similar gross patterns, but the Greenland core exhibits larger, shorter-term fluctuations. The ice buildup from 90,000 years ago to 20,000 years ago was quite variable and was followed by a (geologically speaking) fairly rapid 10,000-year transition,

known as a termination, to the climatically very stable Holocene period. The Holocene is the 10,000-year interglacial period in which human civilization developed and modern plant and animal distributions evolved to their current states (Eddy and Oeschger 1993).

These ice cores also provide information on the presence of CO_2, an important greenhouse-effect gas (Fig. 1). Carbon dioxide was in much lower concentrations during cold periods than in interglacials (which is similar for the greenhouse gas methane, CH_4). This implies an amplifying effect, or a positive feedback, because less of these gases during glacials means less trapped infrared radiative heat amplifying the cooling—and means the reverse during interglacials. The ice cores also show that concentrations of CO_2 and CH_4 and temperature were remarkably constant for about the past 10,000 years (before A.D. 1700), particularly when compared with the longer record. That relative constancy in chemical composition of the greenhouse gases held until the last two centuries—the industrial era.

The transition from Ice Age to the Holocene took from 5,000 to 10,000 years, during which time the average global temperature increased 5°C and the sea level rose 100 meters. Thus, it took nature about 5,000–10,000 years to transform the ice landscape for much of North America and Europe and to transform subpolar seas to their more current conditions in which their permanent ice is restricted to polar seas, high-latitude lands, or high mountains. Because this 5,000- to 10,000-year transition coincides with about a 5°C global warming, we estimate that natural rates of warming on a sustained global basis are about 0.5°C to 1°C per thousand years. Such changes were large enough to have radically influenced where species live and to have potentially contributed to the well-known extinctions of woolly mammoths, saber-tooth cats, and enormous salamanders.

To illustrate the dramatic ecological changes accompanying the Ice Age to the recent interglacial transition, we will briefly describe the findings of a large interdisciplinary team of scientists. The team included ecologists, palynologists (scientists who study pollen), paleontologists (scientists who study prehistoric life, especially fossils), climatologists, and geologists who formed a research consortium known as the Cooperative Holocene Mapping Project (1988; Wright et al. 1993). One group of these researchers used a variety of proxy indicators to reconstruct vegetation patterns over the past 18,000 years for a significant fraction of the Earth's land areas. In particular, cores of fossil pollen from dozens of sites around North America clearly showed how boreal tree pollen, now the dominant pollen type in the boreal zone

Fig. 1. Long-term temperature and CO_2 records from Antarctic ice cores and recent atmospheric measurements. Data show that CO_2 changed in the atmosphere in association with climatic changes over the past 160,000 years, with less of this greenhouse gas occurring in colder periods and more in warmer times (Lorius et al. 1990). For CO_2, the vertical line between the circles represents changes attributable to human activities in the industrial era. For temperature, the line between the circles represents instrumental records of global changes since the Industrial Revolution.

© Nature
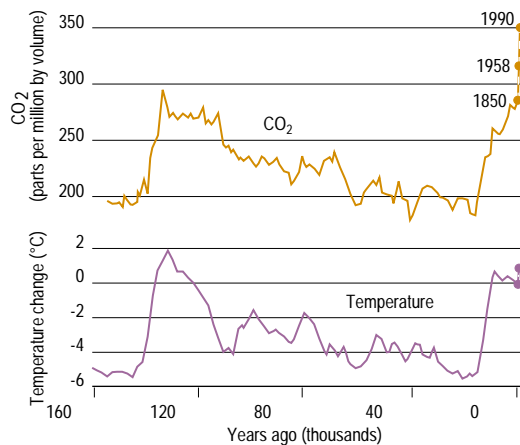
in central Canada, was a prime pollen type during the last Ice Age (15,000–20,000 years ago) in what are now the mixed hardwood and Corn Belt regions of the United States. During the last Ice Age, most of Canada was under ice; pollen cores indicate that as the ice receded, boreal trees moved northward chasing the ice cap. One interpretation of this information was that biological communities moved intact with a changing climate. In fact, Darwin (1859) asserted as much:

> As the arctic forms moved first southward and afterward backward to the north, in unison with the changing climate, they will not have been exposed during their long migrations to any great diversity of temperature; and as they all migrated in a body together, their mutual relations will not have been much disturbed. Hence, in accordance with the principles inculcated in this volume, these forms will not have been liable to much modification.

If this were true, the principal ecological concern over the prospect of future climate change would be that human land-use patterns might block what had previously been the free-ranging movement of natural communities in response to climate change. The Cooperative Holocene Mapping Project, however, incorporated multiple pollen types into its analyses, including not only boreal species but also herbs and more arid (xeric) species, as well as oaks and other mesic species. What they discovered was that during the transition from the last Ice Age to the present interglacial, nearly all species moved north, as expected. During a significant portion of the transition period, however, the distribution of pollen types provided no analog associations to today's vegetation communities (Overpeck et al. 1992). That is, whereas all species moved, they did so individual by individual, not as groups. Consequently, the groupings of species during the transition period were often dissimilar to those present today (Fig. 2). The relevance of this is that in the future ecotypes will not necessarily move as a unit as climate changes (assuming there is time and space enough for such a migration). Past vegetation response to climatic change at an average rate of 1°C per millennium indicates that credible predictions of vegetation changes from comparable or even more rapid climatic changes projected from human activities cannot neglect time-evolving (that is, transient) dynamics of the ecological system.

What is known about the response of various animal taxa to the ice age-interglacial transition? Mammals responded to the last deglaciation in North America by shifting their ranges (Graham 1992; Fig. 3) relatively quickly (Graham and Mead 1987). Graham and Grimm (1990), however, cautioned against relying too much on past conditions in forecasting future patterns resulting from global change forcings, because the forecasted global average rate of temperature increase exceeds those rates typical of the last 120,000 years, a conclusion consistent with the results of the Cooperative Holocene Mapping Project researchers studying vegetation communities (Davis 1990).

Future climates may not only be quite different from more recent previous climates but may also be different from those inferred from paleoclimatic data and from those to which some existing species are evolutionarily adapted. Therefore, possible future changes inferred from past changes can be taken only as a guide or a means to verify aspects of the forecasts of models of climate or ecosystem dynamics (Crowley 1993; Schneider 1993a). Such verification exercises may provide more credible forecasts of the effects of climatic change on animals.

Why Climate Changed

The two basic categories of causes of climatic change are external and internal. External causes mean that the climate change arises outside of the system and it is not influenced much by the system, although external processes do not have to be physically external to the Earth (such as the sun). If our focus is on atmospheric change on a 1-week time scale (that is, the weather), the oceans, land surfaces, biota, and human activities that produce CO_2 are all external (that is, they are not influenced much by the atmosphere in such a short time). If our focus is on 100,000-year ice age interglacial cycles, however, the oceans, ice sheets, and biota are part of the internal climatic system and vary as an integral part of the Earth's environmental systems. On this longer scale we must also include as part of our internal system the "solid" Earth, which really is not solid but viscous and elastic. Therefore, stating which components are external or internal to the climatic system depends on the time period and spatial scale being examined, as well as on the phenomena being considered.

Fluctuations in heat radiated by the sun—perhaps related to varying sun spots—are external to the climate system. Influences of the gravitational tugs of other planets on the Earth's orbit are also external. Many researchers think that such tugs gave rise to the 40,000-year ice cycle in the past 2.5 million years and possibly contributed to the 100,000-year ice age and interglacial cycles as well (Imbrie et al. 1993). Human-caused
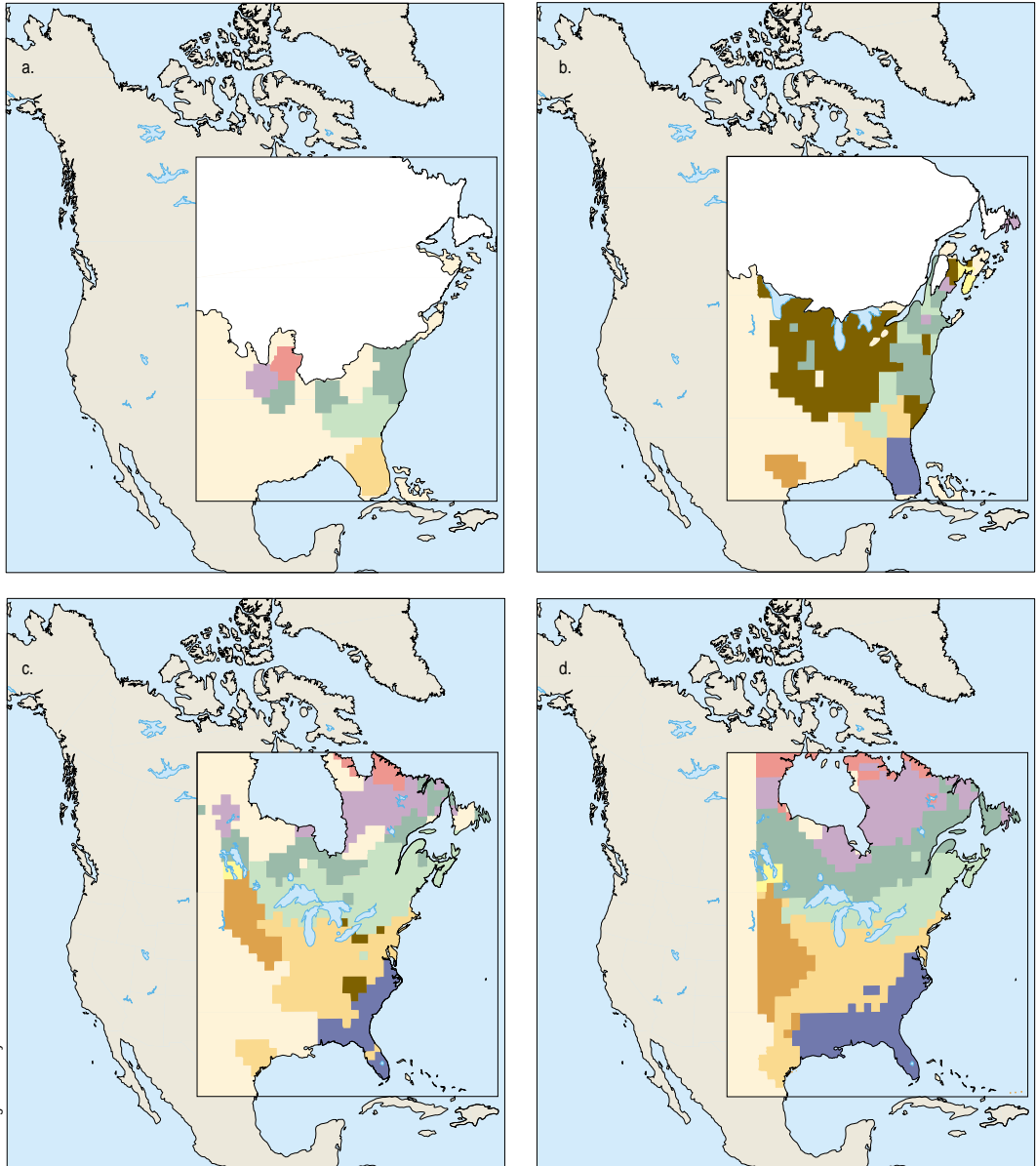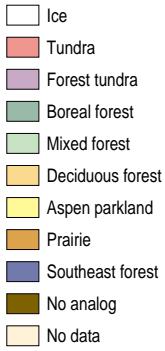
Ice
Tundra
Forest tundra
Boreal forest
Mixed forest
Deciduous forest
Aspen parkland
Prairie
Southeast forest
No analog
No data

© Geological Society of America

Fig. 2. Selected paleovegetation maps reconstructed by using the method of modern analogs and more than 13,000 samples of fossils and modern pollen. a) 18,000 B.P., b) 12,000 B.P., c) 6,000 B.P., and d) modern. No vegetation is mapped in areas without fossil pollen data, and no analog refers to vegetation without any modern analog (Overpeck et al. 1992).

© Yale University Press

Fig. 3. Modern distribution (orange area) of Greenland collared lemmings and fossil localities (red dots) that illustrate the southern extension of their distribution during the late Wisconsinan. Purple line marks Wisconsinan glacial maximum (Graham 1992).

changes in the Earth's climate could not perceptibly alter either one of these cycles.

Changes in volcanic dust or CO_2 in the atmosphere also influence climate; volcanic dust can cool the climate by scattering some sunlight back to space, and CO_2 can warm the climate through the greenhouse effect. On short time scales, these factors are largely external because the state of the climatic system presumably does not have much influence on them. This may not be true, though, in the long term. For example, the tendency for volcanoes to erupt might change when the Earth's crust is distorted by the weight of ice sheets. Likewise, if the climate changes in such a way that an area previously covered with plants becomes drier, dust can be raised more easily. Thus, on the long-term scale, dust generation falls into the internal category.

Carbon dioxide and methane levels rise and fall with ice age cycles (Fig. 1), which are clearly internal on a 10,000-year time scale. But on a 20-year scale these greenhouse gases become largely an external cause of climatic change, because small changes in climate have little feedback effect on, for example, humans burning fossil fuel.

Changes in the character of the land surface, if caused by human activities, are largely external. If vegetation cover changes because of climatic change, however, land surface change then becomes internal because changes in plant cover can influence the climate by changing albedo (reflectivity to sunlight), evapotranspiration, surface roughness, and relative humidity (Henderson-Sellers et al. 1993).

Snow and ice are important factors in climatic change because they have higher albedo (reflectivity) than warmer surfaces and, in the instance of sea ice, can inhibit transfer of heat and moisture between air and wet surfaces. Salinity, which affects changes in sea ice and in the density of seawater (which helps control where ocean waters sink), may also be an internal cause of climatic variation. The sinking and upwelling of ocean waters are biologically significant because the upwelling waters are often nutrient-rich.

Unusual patterns of ocean surface temperature—such as the El Niño—demonstrate the importance of internally caused climatic fluctuations because the atmospheric circulation can change simultaneously with ocean surface temperatures. The atmosphere rubs on the ocean, however, so the ocean responds with a modification in its motions and temperature pattern, which forces the atmosphere to adjust, which changes the winds, which changes the way the atmosphere rubs on the ocean, and so forth (Trenberth 1993). As a result, air and water interact internally in this coupled system like blobs of gelatin of different size and stiffness, connected by elastic bands or springs, all interacting with one another while also being pushed from the outside (by solar, volcanic, or human-caused change).

Credibility of Climate Change Forecasts

To predict the ecologically significant ways the climate might change, one must specify what people do that modifies how energy is exchanged among the atmosphere, land surface, and space because such energy flows are the driving forces behind climate. Making the atmosphere window dirtier through air pollution is an example of such a so-called societal forcing of the climate system. Estimating societal forcing involves forecasting a plausible set of human (or societal) activities affecting pollution over the next century. The next step is to estimate the response of the various components of the Earth system to such societal forcings. The Earth system itself consists of the following interacting subcomponents: atmosphere, oceans, cryosphere (snow, seasonal ice, and glaciers) and land-surface (biota and soils) systems.

Research in the field and in laboratories provides an understanding about various processes affecting the subcomponents of the Earth system. This understanding can be put into mathematical expressions, which, when combined, form a model of the behavior of particular components of the Earth system. In practice, models of the atmosphere are connected to models of the oceans, ice, biota, and land surfaces to simulate the consequences of some scenario of societal forcing on climate and ecosystems. Controversy arises because both the societal forcing that will actually occur and the scientific knowledge of each subsystem are still incomplete. Because models cannot be perfect replicas of the actual natural system, scientists must expend considerable efforts to test their models against the expanding base of field and laboratory data. This not only allows them to assess the credibility of current simulations, but it also reveals improvements for the next generation of models.

Elements of Global Warming Forecasts

The societal driving forces behind global-warming scenarios are projections of population, consumption, land use, and technology. Typical twenty-first century projections for human population size and affluence for less highly developed countries and more highly developed countries show drastic increases in population and wealth (Fig. 4). When these factors are multiplied by the amount of energy used to produce a unit of economic product (the so-called energy intensity) and the amount of CO_2 emitted per unit of energy (the technology factor called carbon intensity), the result is a forecast for carbon emissions in the twenty-first century. For the particular projections shown in Figures 4 and 5 (from Bongaarts 1992), CO_2 emissions rise severalfold over the next 100 years. Such specific scenarios are plausible but debatable because the amount of carbon emitted through human activities will significantly depend on what kinds of energy systems will be developed and deployed globally and on what the standards of living will be over the next several decades. It is very difficult to make such projections credibly; therefore analysts disagree by as much as a factor of 10 about how much CO_2 will be emitted by 2100 (Johansson
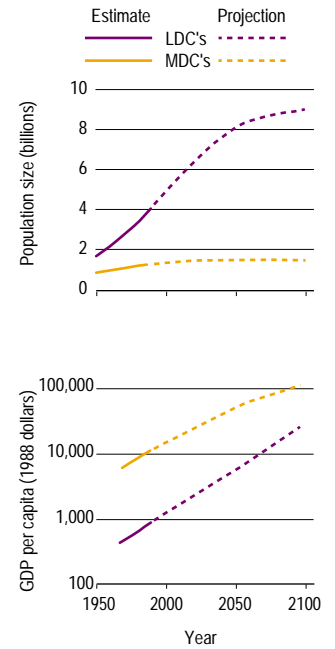
Fig. 4. Estimates and projections of population size and gross domestic product (GDP) per capita for less highly developed countries (LDC's) and more highly developed countries (MDC's) for 1950–2100 (Bongaarts 1992).

© Population and Development Review

Fig. 5. Estimates and projections of energy and carbon intensities for less highly developed countries (LDC's) and more highly developed countries (MDC's) for 1965–2100 (Bongaarts 1992).
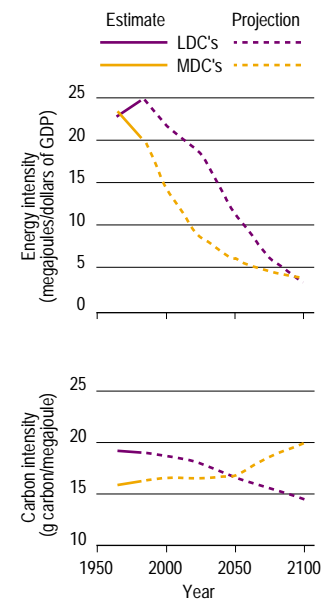
© Population and Development Review

et al. 1993; Intergovernmental Panel on Climate Change 1996a,c).

To turn estimates of CO_2 emissions into estimates of CO_2 concentrations in the atmosphere—the variable needed to calculate potential climate changes—one must estimate what fraction of CO_2 emitted will remain in the atmosphere. This airborne fraction is most simply estimated at 50%, because the amount of CO_2 buildup in the atmosphere each year (about 3 billion tons of carbon as CO_2) is about half the fossil fuel-injected CO_2. The atmospheric concentration of CO_2 should, however, be computed by using carbon cycle models, which account for the time-evolving amounts of carbon in vegetation, soils, oceanic, and atmospheric subcomponents (Intergovernmental Panel on Climate Change 1996a,b). The estimated CO_2 concentration can then be fed into computerized climatic models to estimate its effects on climate.

Climate prediction, like most other forecasts involving complex systems, generally involves educated guesses. Those attempting to determine the future behavior of the climate system from knowledge of its past behavior and present state basically can take two approaches. One approach, the empirical–statistical, uses statistical methods such as regression equations that connect past and present observations statistically to obtain the most probable extrapolation. The second approach, usually called climate modeling, focuses on first principles, which are equations representing laws believed to describe the physical, chemical, and biological processes governing climate. Because the statistical approach depends on historical data, it is obviously limited to predicting climates that have been observed or are caused by processes appropriately represented in the past conditions. The statistical method cannot reliably answer questions such as what would happen if atmospheric CO_2 increased at rates much faster than in the known past. Thus, the more promising approach to climate prediction for conditions or forcings different from the historic or ancient past is climate modeling. A significant component of empirical–statistical information, though, is often embedded into these models (Washington and Parkinson 1986; Root and Schneider 1995). This often makes modelers uncomfortable about the validity of predictions of such models on unusual or unprecedented situations unless a great deal of effort is expended to test the models against present and paleoclimatic baseline data.

Climate models vary in their spatial resolution, that is, the number of dimensions they simulate and the spatial detail they include. The simplest model calculates only the average temperature of the Earth, independent of the average greenhouse properties of the atmosphere. Such a model is zero-dimensional—it reduces the real temperature distribution on the Earth to a single point, a global average. In contrast, three-dimensional climate models produce the variation of temperature with latitude, longitude, and altitude. The most complex atmospheric models, the general circulation models, predict the time evolution of temperature plus humidity, wind, soil moisture, sea ice, and other variables through three dimensions in space (Washington and Parkinson 1986).

Relevance to Ecosystem Studies

Scientists who estimate the future climatic changes that are relevant to ecosystems have focused on the general circulation models that attempt to represent mathematically the complex physical and chemical interactions among the atmosphere, oceans, ice, biota, and land. As these models have evolved, more and more information has become available, and more comprehensive simulations have been performed. Nevertheless, the complexities of the real climate system still vastly exceed the general circulation models and the capabilities of even the most advanced computers (Intergovernmental Panel on Climate Change 1990, 1996a,b). Simulating one year of weather in 30-minute time steps with the crude resolution of 40 latitudinal lines x 48 longitudinal lines and 10 vertical layers—nearly 20,000 grid cells around the globe—takes about 10 hours on a supercomputer (the Cray Y-MP, for example). This level of resolution, however (Fig. 6), cannot resolve the Sierra Nevada of California and the Rocky Mountains as separate mountain chains. Refining the resolution to 50-square-kilometer grid squares would so dramatically increase the number of computations that it would take roughly one year of computer time to simulate weather statistics for one year.

What is most needed to evaluate potential biological effects of temperature change is a regional projection of climatic changes that can be applied to ecosystems at a regional or local scale. Analyses of large, prehistoric climatic changes (Barron and Hecht 1985; Budyko et al. 1987; Schneider 1987; Cooperative Holocene Mapping Project 1988) and historical weather analogs (Pittock and Salinger 1982; Jager and Kellogg 1983; Lough et al. 1983; Shabalova and Können 1995) provide some insights into such changes. Historical weather analogs, however, since they are empirically and statistically based, rely on climatic cause-and-effect processes that probably differ from those that will be driven by future greenhouse gas radiative effects (Schneider 1984; Mearns et al. 1990; Crowley 1993). Consequently, ecologists turn to climatic models to produce forecasts of

regional climatic changes for the decades ahead. How credible are such forecasts?
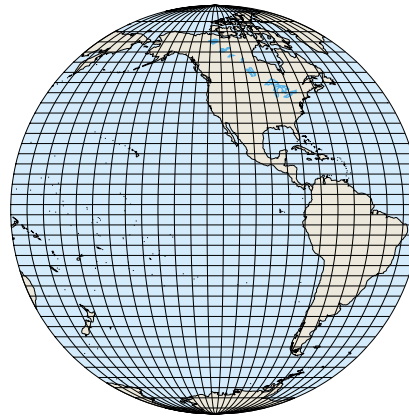
Regional Changes

Although the consensus among researchers about the plausibility of significant human-induced global climatic change is growing, no assessment (Intergovernmental Panel on Climate Change 1996a) has suggested the existence of a strong consensus about how that global climatic change might be distributed regionally. For example, the world is not actually undergoing a dramatic and instantaneous doubling of CO_2, which is the hypothesis used in most standard computer model experiments applied to ecological assessments. Instead, the world is undergoing a steady increase in greenhouse gas forcing. Because that increase is heating the Earth in a reasonably uniform way, one might expect a uniform global response, though this is far from likely. For example, the centers of continents have relatively low heat-retaining capacity, and the temperatures there would move relatively rapidly toward whatever their new equilibrium climate would be compared with the centers of oceans, which have high heat-retaining capacity. Tropical oceans, though, have a thin (about 50 meters) mixed layer that interacts primarily with the atmosphere. It takes about 10 years for that mixed layer to substantially change its temperature, which is still much slower than the response time of the middle of the continents, but is much faster than that of the oceans closer to the poles. At high latitudes, in places like the Weddell or Norwegian seas, waters can mix down to the bottom of the ocean, thereby continuously bringing up cold water and creating a deepwater column that takes a century or more to substantially change its temperature.

During the transient phase of climate change over the next century, therefore, one would expect the middle of continents, the middle of oceans, and the polar and subpolar oceans all to change toward their new equilibrium temperatures at different rates. Thus, the temperature differences from land to sea and equator to pole will evolve over time, which, in turn, implies that the transient character of regional climatic changes could be very different from the expected long-term equilibrium (Schneider and Thompson 1981; Stouffer et al. 1989; Washington and Meehl 1989). This does not imply that transient regional changes are inherently unpredictable, only that at present they are very difficult to predict credibly.

Even more uncertain than regional averages, but perhaps more important to long-term ecosystem responses, are estimates of climatic variability during the transition to a new equilibrium, particularly at the regional scale. These
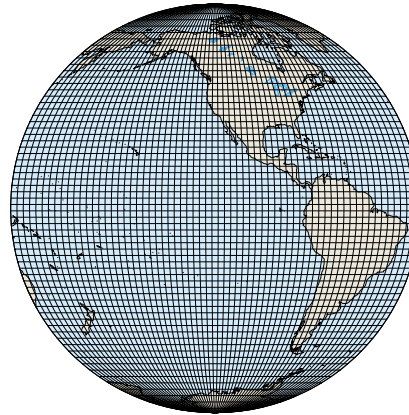

a. 40 latitude x 48 longitude (1,920 total grid cells)   b. 54 latitude x 64 longitude (3,456 total grid cells)
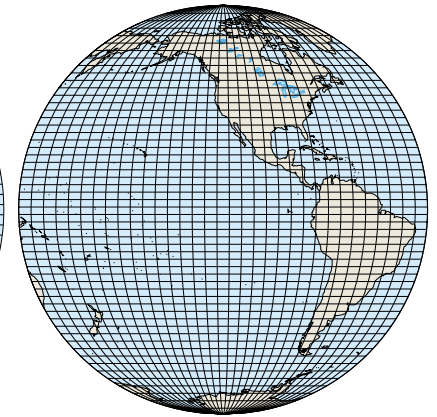
c. 64 latitude x 128 longitude (8,192 total grid cells)   d. 144 latitude x 288 longitude (41,472 total grid cells)

include estimates of such events as the frequency and magnitude of severe storms, enhanced heat waves, temperature extremes, sea-level rises (Titus and Narayanan 1995), and reduced frost probabilities (Mearns et al. 1984, 1990; Parry and Carter 1985; Wigley 1985; Rind et al. 1989). For example, there is a physical principle that evaporation increases dramatically as surface-water temperature increases. Because hurricanes are powered by evaporation and condensation of water, if all other factors are unchanged, the intensity of hurricanes and the length of the hurricane season could increase with warming of the oceans (Emanuel 1987). Such changes would significantly affect susceptible terrestrial and marine ecosystems (Doyle 1981; O'Brien et al. 1992).

Verifying Climate Forecasts

The most perplexing question about climate models is whether they can be trusted as a reliable basis for altering social policies, such as those governing CO_2 emissions or the shape and location of wildlife reserves. Even though these models are fraught with uncertainties, several methods are available for verification tests. Although no method is

Fig. 6. The fineness of a climate model's grid size affects the accuracy of the simulations as well as the level of detail in the climate simulation that can be used for ecological applications. The information above each model shows the number of latitude and longitude lines for each grid-cell size and how many such cells cover the Earth's surface at the specified resolution. Most climate models use resolutions a, b, or c because computational resources increase by more than a factor of ten each time the length of a grid cell's side is halved. a) Grid R15, b) grid R21, c) grid T42, and d) grid T95.

sufficient by itself, several methods together can provide significant, albeit circumstantial, evidence of a forecast's credibility.

The first validation testing method involves checking the model's ability to simulate the present climate. The seasonal cycle is one good test because temperature changes in a seasonal cycle are larger on a hemispheric average than the change from an ice age to an interglacial period (that is, 15°C seasonal range in the Northern Hemisphere versus 5°C glacial-interglacial cycle). General circulation models map the seasonal cycle well (Fig. 7), which suggests that their mid- to high-latitude surface-temperature sensitivity to large-scale radiative forcing is not in error by more than a factor of three. This helps explain the scientific consensus about the plausibility of global warming of several degrees in the twenty-first century. The seasonal test, however, does not indicate how well a model simulates slow processes such as changes in deep ocean circulation, ice cover, forests, or soil carbon storage, which may have important effects on the decade- to century-long time scales over which atmospheric CO_2 is expected to double.
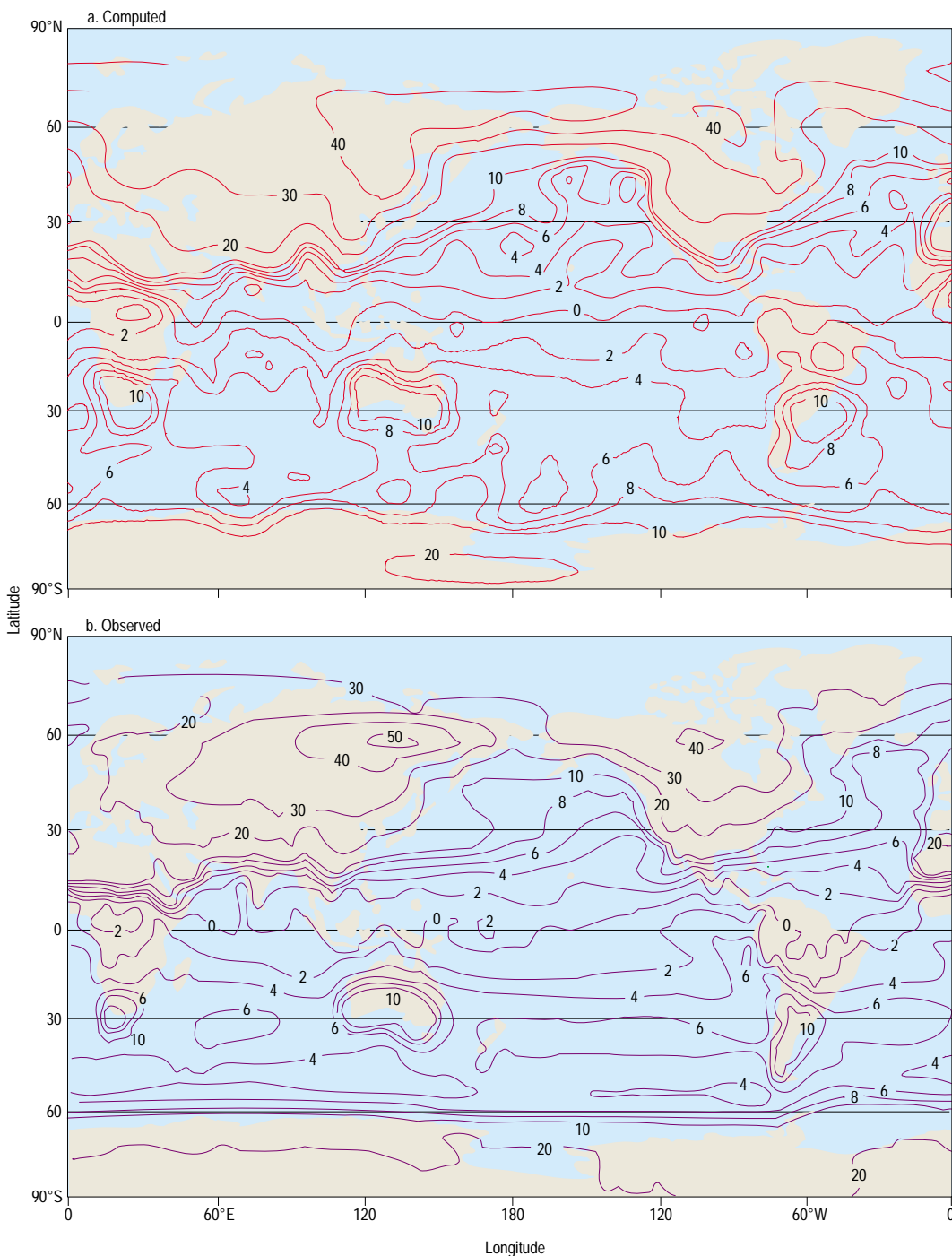

Fig. 7. A three-dimensional climate model was used to compute the absolute temperature difference between January and July over the globe. The a) computed model reproduces many of the features of the b) observed seasonal cycle shown here (Manabe and Stouffer 1980).

A second verification technique involves isolating individual physical components of the model and testing them against actual data. For example, one can check whether the model's cloudiness statistics match the observed cloudiness statistics of a particular area and season. This technique, though, cannot guarantee that the complex interactions of individual model components are properly treated. For example, the model may be reliable at predicting average cloudiness but unreliable at representing how cloudiness might change with a change in climate (the so-called *cloud feedback problem*). In this instance, simulation of overall global climatic response to some parameter like increased CO_2 is likely to be inaccurate. A model should reproduce the flow of thermal energy among the atmosphere, the surface, and space with no more than about a 10% error. Together, these energy flows make up the well-established natural greenhouse effect on Earth and constitute a formidable and necessary test for all models. A model's performance in simulating these energy flows is an example of physical validation of model components. In one encouraging example, Raval and Ramanathan (1989) used satellite observations to compute the infrared heat-trapping capacity of the atmosphere (that is, the natural greenhouse effect) with increased surface temperature. Next, they made a similar calculation between the heat-trapping-effect calculations in the general circulation model and compared this with satellite observations, finding that the models performed very well in this test.

A third validation method involves the model's ability to reproduce the diverse climates of the past. This method is aided by recording instrumental observations made during the past few centuries and paleo-records that serve as a proxy for climatic conditions of the ancient Earth, or even include testing models' ability to simulate climates of other planets (Kasting et al. 1988). Paleoclimatic simulations of the Mesozoic (Age of the Dinosaurs), glacial-interglacial cycles, or other extreme past climates help scientists understand the coevolution of the Earth's climate and living things (Schneider and Londer 1984). As verification tests of climate models, they are also crucial to predicting future climates and changes in biological systems.

Much has been learned from examining the global climatic trends of the past century. The years 1990 and 1995 were the warmest years on record for the lower atmosphere in the past century (Fig. 8); at the same time the stratosphere was at its coldest (Intergovernmental Panel on Climate Change 1996a). These data are consistent with an enhanced greenhouse effect signal that might be anticipated from the greenhouse
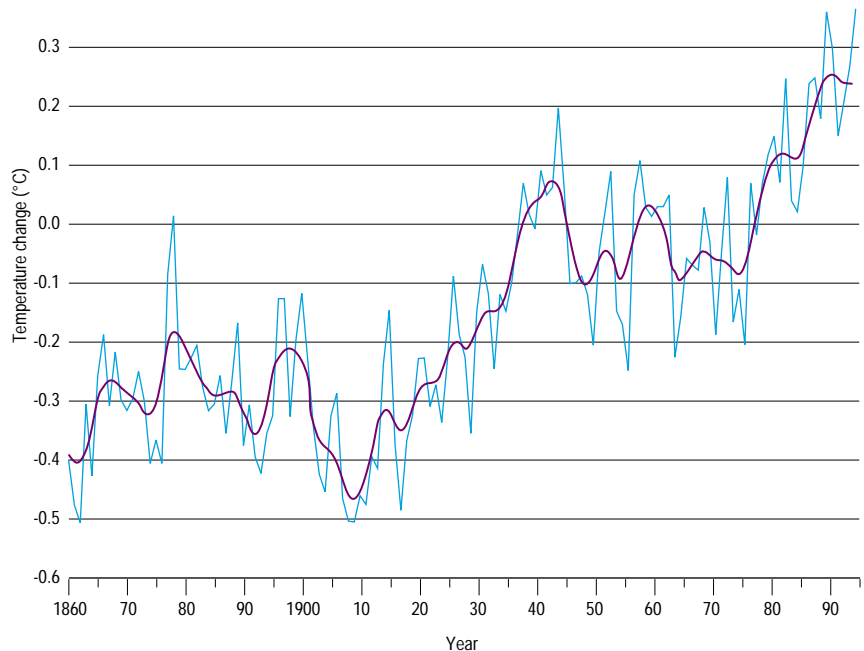

gas injections over the past 150 years, which saw a 25% increase in CO_2, a 150% increase in CH_4, and the introduction of human-generated heat-trapping chemicals such as chlorofluorocarbons and halons. Most scientists still argue that, although the $0.5°C \pm 0.2°C$ surface warming in the twentieth century is consistent with the human-induced greenhouse gas buildup, it is not possible to state with 99% confidence that the observed warming was caused by that greenhouse gas forcing (Intergovernmental Panel on Climate Change 1996a). It is possible—although at a relatively low probability of 10%–20% (Schneider 1994)—that the 0.5°C warming trend was wholly natural and that there was little or no contribution from the buildup of greenhouse gases (for estimates of the probability of global warming amounts, see Morgan and Keith 1995).

Of course, if one cannot tell whether an unforecastable natural fluctuation in climate in the twentieth century could have created the bulk of the observed warming, then one equally cannot tell whether there was a natural cooling fluctuation taking place during the twentieth century. If so, the world would then have warmed up much more than observed had we not had a fortuitous natural cooling trend. One could even speculate that the dramatic temperature rise in the 1970's and all of the associated new warm global temperature records reflect the termination of a natural cooling trend combined with the rapid establishment of the expected enhanced greenhouse effect.

One important possibility that could have helped create the twentieth-century temperature record seen in Figure 8 is the generation of aerosol particles (for example, human-made or

Fig. 8. The record of past global warming in observed global mean temperature changes, 1860–1995 (Intergovernmental Panel on Climate Change 1996a data). The purple line is the 5-year running mean; the blue line represents the annual values.

induced by natural sulfur dioxide) floating in the atmosphere that could either directly or indirectly reflect sunlight to space. The aerosol particles, through incorporation into clouds, could increase the number of water droplets, making some clouds brighter. Measurements and theory are not yet adequate to describe the latter mechanism quantitatively, although some attempts are under way (Kaufman et al. 1993). Charlson et al. (1992) suggested that industrial activities since the 1950's offset some of the greenhouse surface heating by countering it with some atmospheric cooling from haziness around and downwind of sulfur-burning areas in the Northern Hemisphere. Although such sulfur dioxide-induced cooling may have opposed any global warming by several tenths of a degree, the hazes occur regionally and could be producing ecologically significant, unexpected regional changes in climate patterns (Schneider 1994).

Recent studies (Santer et al. 1996) suggest that when aerosols and greenhouse gas forcings are combined, climatic change patterns in models over the past 30 years of observations match much more closely. Nevertheless, all these possibilities render current observations consistent with a CO_2 doubling effect of anywhere from as low as a 0.5°C warming to as high as a 5.0°C warming (Wigley and Raper 1991). Several reasons exist for such a wide range of uncertainty: difficulty in knowing how to model delays in global warming because of the large heat capacity of the oceans; not knowing what other global change forcings may have opposed warming—for example, sulfate aerosols from burning high-sulfur coal and oil or undetectable changes in the sun's light output before 1980; and large, unknown, internal natural climatic fluctuations.

In summary, no clear physical objection or direct empirical evidence has contradicted the consensus of scientists (Intergovernmental Panel on Climate Change 1990, 1996a) that the world is warming, nor has evidence emerged to contradict the substantial probability that temperatures will rise because of increases in greenhouse gases (Morgan and Keith 1995). The evidence for current global warming forecasts is circumstantial, but is sufficient enough that many researchers believe that recently observed climatic variations and human activities are probably connected (Karl et al. 1995). The Intergovernmental Panel on Climate Change 1996a:5 carefully weighed the uncertainties and concluded that "Nevertheless, the balance of evidence suggests that there is a discernable human influence on global climate."

The consensus remains widespread that a global temperature increase of anywhere from 1°C to 5°C is reasonably probable in the next century. The Intergovernmental Panel on Climate Change (1990), which reflects the consensus of hundreds of scientists in the United States and elsewhere, used a five-star rating system to describe various possibilities for global warming, one star being least likely and five stars most likely. The scientists gave global average temperature changes (from CO_2 doubling) ranging from 1.5°C to 4.5°C three stars, equivalent presumably to a 60% subjective chance. The Intergovernmental Panel on Climate Change (1996a) saw no reason to alter that assessment. As mentioned previously, though, the ecologically important forecasts of time-evolving regional climatic changes are much less credible and require that ecologists use many alternative scenarios of possible climatic changes.

Estimating the Effects of Climate Change on Ecosystems

Even the highest-resolution, three-dimensional general circulation model will not have a grid with nodes much less than 100 kilometers apart within the foreseeable future; individual clouds and most ecological research (to say nothing of cloud droplets) occur on scales far smaller than that. Therefore, general circulation models will not be able to resolve the local or regional details of weather affecting most local biological communities or the importance of regional effects of hills, coastlines, lakes, vegetation boundaries, and heterogeneous soil (Root and Schneider 1993). It is, nonetheless, important to have climatic forecasts and ecological response analyses on the same physical scales.

Shrinking Climate Forecasts to Regional Scales

Empirical Mapping Techniques

Techniques exist that can translate the output of climate models so that it is closer to most ecological scales. One method that uses actual climatic data at both large and small scales can help provide maps that may allow small-scale analysis of large-scale climate change scenarios. For example, the Sierra Nevada of California or the Cascades in the northwestern United States are north-south mountain chains whose east-west dimensions are smaller than the grid size of a typical general circulation model. In the actual climate system, onshore winds on the Pacific coast would produce cool upslope and rainy conditions on the western slope and a high probability of warmer and drier conditions associated with that flow pattern on the downslope or eastern slope.

One regional map has been generated for Oregon (Gates 1985), in which a high-resolution network of meteorological stations was used to plot temperature and precipitation

isopleths based on observed climatic fluctuations at large (for example, state-sized) scales. These maps show that the dominant mode of variation for this area is warm and dry on one side of the mountains, cold and wet on the other. Although this empirical mapping technique seems appropriate for translating low-resolution, grid-scale climate model forecasts to local applications, a strong caveat must be offered. That is, the processes in the climate system that give rise to internal variability or natural fluctuations are not necessarily the same processes that would give rise to local deviations from large-scale patterns if the climate change were driven by external forces rather than an internal variation of the system. For example, the Oregon maps would indicate that if the grid-box average temperature were warmer on the eastern slope, then it should be cooler and wetter on the western slope. That condition is the most probable regional situation for today's naturally fluctuating climate. However, if 50 years from now the warming on the eastern slope were, say, a result of doubled atmospheric CO_2 causing an enhanced downward infrared radiative heating, then both eastern and western slopes would probably experience warming. Although the degree of warming and associated precipitation changes would not necessarily be uniform, an entirely different climatic change pattern would probably occur as opposed to that obtained from the empirical mapping technique if one used the naturally varying weather conditions existing today rather than the anthropogenically forced conditions of the twenty-first century (Schneider 1993b).

Therefore, techniques to shrink climate forecasts that use current distributions of environmental variables at local scales and correlate them with current large-scale regional patterns will not necessarily provide a good guideline about how large-scale patterns would be distributed locally. The reason is that the causes of the future change may be physically or biologically different from the causes of the historical fluctuations that led to the empirical maps in the first place. This caveat is so important that it requires scientists to use extreme caution before adopting such empirical techniques for global change applications.

Driving Regional-Scale Models with Large-Scale Forecasts

Other techniques can still translate large-scale patterns to smaller scales, but these techniques are based on known processes rather than empirical maps for today's conditions. One such technique is to drive a high-resolution, process-based model for a limited region with the large-scale patterns produced by a general circulation model. In essence, this approach uses a mesoscale model (that is, 10–50 square-kilometer grid cells) based on physical laws to solve the problem of translating general circulation model grid-scale averages into a finer scale mesh much closer to the dimensions of most ecological applications. Of course, even this mesoscale grid will still be too coarse to assess many impacts, necessitating further down-scaling techniques. Neither are the problems of general circulation models entirely eliminated by mesoscale grids, because they too are bigger than individual clouds or trees. But such methods do bring climate model scales and ecological-response scales much closer.

Giorgi (1990) and colleagues at the National Center for Atmospheric Research have worked many years with this embedding technique. They have noted, for example, that a general circulation model with a very coarse grid that is unable to resolve the separate topographies of the Sierra Nevada and the Rocky Mountains (and therefore is unable to produce the rain shadow of the Great Basin) may still produce reasonably accurate simulations of large-scale wind and moisture patterns. By using the large-scale wind and moisture fields of the general circulation model to drive a mesoscale model with a factor of 10 higher resolution (capable of resolving much of these mountain and desert topographies), these researchers were able to reproduce much more realistically the regional distribution of current climatic conditions. Therefore, such a process-based technique could be used to translate general circulation model grid-box scenarios into at least watershed-scale changes that would be closer to the scale of ecological studies than current general circulation model grids.

Unfortunately, even this process-based technique has several serious problems yet to be solved. First, these models use about as much computer time to simulate several days of weather at regional scales as the general circulation model needs for simulating one year of weather globally. Second, the mesoscale model results depend on validity of the overall flow patterns from the large-scale models. If the latter exhibit roughly the right direction for prevailing wind and moisture flow, the smaller-scale model will more faithfully translate that large-scale pattern down to regional detail.

A new technique combining empirical and process-based approaches to translate general circulation model grid predictions of doubling CO_2 climate changes to 10-square-kilometer grid cells was developed by Stamm and Gettelman (1995) and is called a local climate model. Although they obtained encouraging results for local climate deviations in the highly varying topography of the western United States, Stamm and Gettelman found that their

technique has difficulty estimating ecologically important extreme (high or low) temperatures or extreme precipitation events. Resolving these difficulties with current techniques is critical to the utility of the local climate model for ecological impact assessment. Other downscaling techniques are summarized in Mearns (1997).

Examples of Ecological Responses to Climate Changes

Bringing climatic forecasts down to ecological applications at local and regional scales is one way to bridge the scale gap across ecological and climatological studies. Ecologists, however, have also analyzed data and constructed models that apply over large scales, including the size of climatic model grids. A long tradition in ecology has associated the occurrence of vegetation types or the range limits of different species with physical factors such as temperature, soil moisture, land–sea boundaries, or elevation. Biogeography is the field that deals with such associations, and its results have been applied to estimate the large-scale ecological response to climate change.

Predicting Vegetation Responses to Climate Change

The Holdridge (1967) life-zone classification assigns biomes (for example, tundra, grassland, desert, or tropical moist forest) according to two measurable variables, temperature and precipitation (Fig. 9). Other more complicated large-scale formulas have been developed to predict vegetation patterns from a combination of large-scale predictors (for example, temperature, soil moisture, or solar radiation); vegetation modeled includes individual species (Davis and Zabinski 1992), limited groups of vegetation types (Box 1981), or biomes (Prentice 1992; Melillo et al. 1993; Neilson 1993). These kinds of models predict vegetation patterns that represent the gross features of actual vegetation patterns, which is an incentive to use them to predict vegetation change with changing climate. Smith et al. (1992) show an example of a vegetation model's prediction of changes given the forecast of doubled CO_2 from a climate model (Fig. 10).

As we explore in more detail later, such models have limitations. One criticism of such
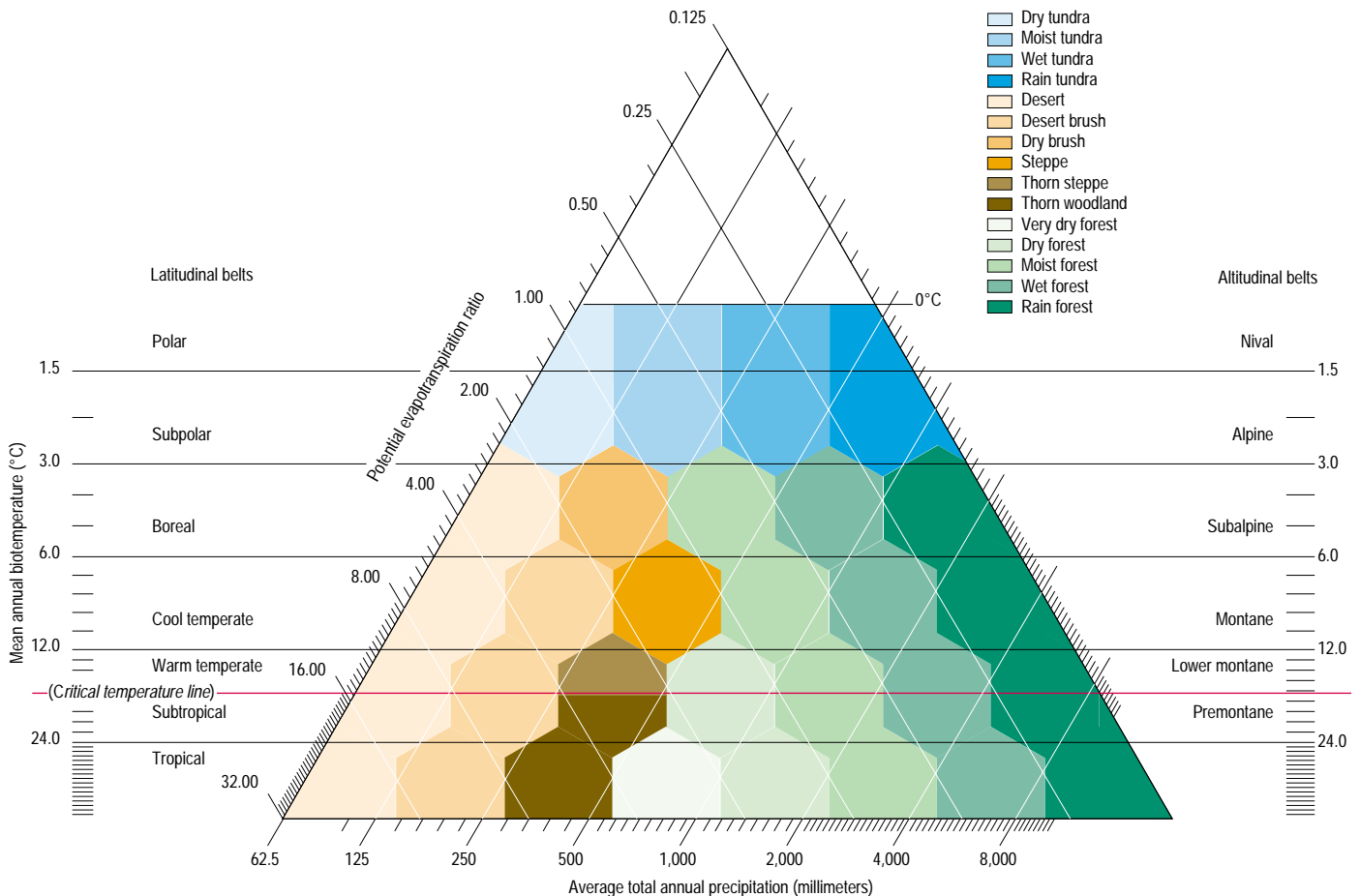

Fig. 9. Holdridge's (1967) climate–vegetation classification scheme.

large-scale approaches is that, although the climate or other large-scale environmental factors are favorable to some biome that is actually present, these approaches also often predict vegetation to occur where it is absent. Other criticisms are aimed at the static nature of such models, which often predict vegetation changes to appear instantaneously at the moment the climate changes, neglecting transient dynamics that often cause a sequence or succession of vegetation types to emerge over decades to centuries following some disturbance (for example, fire), even in an unchanging climate.

Predicting Animal Responses to Climate Change

Scientists of the U.S. Geological Survey, in cooperation with Canadian scientists, conduct the annual North American Breeding Bird Survey, which provides distribution and abundance information for birds across the United States and Canada. From these data, collected by volunteers under strict guidance from the U.S. Geological Survey, shifts in bird ranges and abundances can be examined. Because these censuses were begun in the 1960's, these data can provide a wealth of baseline information. Price (1995) has used these data to examine the birds that breed in the Great Plains. By using the present-day ranges and abundances for each of the species (Fig. 11a), Price derived large-scale, empirical–statistical models based on various climate variables (for example, maximum temperature in the hottest month and total precipitation in the wettest month) that provided estimates of the current bird ranges and abundances (Fig. 11b). Then, by using a general circulation model to forecast how doubling of CO_2 would affect the climate variables in the models, he applied the statistical models to predict the possible shape and location of the birds' ranges and abundances (Fig. 11c).

Significant changes were found for nearly all birds examined. The ranges of most species moved north, up mountain slopes, or both. The empirical models assume that these species are capable of moving into these more northerly areas, that is, if habitat is available and no major barriers exist. Such shifting of ranges and abundances could cause local extinctions in the more southern portions of the birds' ranges, and, if movement to the north is impossible, extinctions of entire species could occur. We must bear in mind, however, that this empirical–statistical technique, which associates large-scale patterns of bird ranges with large-scale patterns of climate, does not explicitly represent the physical and biological mechanisms that could lead to changes in birds' ranges. Therefore, the detailed maps should be viewed only as illustrative of the potential for very

significant shifts with different possible doubled CO_2 climate change scenarios. More refined techniques that also attempt to include actual mechanisms for ecological changes are discussed later.

Reptiles and amphibians, which together are called herptiles, are different from birds in many ways that are important to our discussion. First, because herptiles are ectotherms—meaning their body temperatures adjust to the ambient temperature and radiation of the environment—they must avoid environments where temperatures are too cold or too hot. Second, amphibians must live near water, not only because the reproductive part of their life cycle is dependent on water, but also because they must keep their skin moist because they breathe through their skin as well as their lungs. Third, herptiles are not able to disperse as easily as birds because they must crawl rather than fly, and the habitat through which they crawl must not be too dry or otherwise impassable (for example, high mountains or superhighways).

As the climate changes, the character of extreme weather events, such as cold snaps and droughts, will also change (Karl et al. 1995), necessitating relatively rapid habitat changes for most animals. Rapid movements by birds are possible since they can fly, but for herptiles such movements are much more difficult. For example, R. L. Burke (University of Michigan, Ann Arbor, personal communication) noted that during the 1988 drought in Michigan, many more turtles than usual were found dead on the roads. He assumed they were trying to move from their usual water holes to others that had not yet dried up or that were cooler (for example, deeper). For such species, moving across roads usually means high mortality. In the long term, most birds can readily colonize new habitat as climatic regimes shift, but herptile dispersal (colonization) rates are slow. Indeed, some reptile and amphibian species may still be expanding their ranges north even now, thousands of years after the last glacial retreat.

R. L. Burke and T. Root (personal communication) have begun analyzing North American herptile ranges in an attempt to determine which, if any, are associated with climatic factors such as temperature, vegetation-greening duration, solar radiation, and so forth. Their preliminary evidence indicates that northern boundaries of some species ranges are associated with these factors (Fig. 12), implying that climatic change could have a dramatic impact on the occurrence of herptile species. It could also alter the population genetics within species since there can be genetic differences among populations with respect to climate tolerance. Many more extinctions are possible in herptiles than in birds because the forecasted
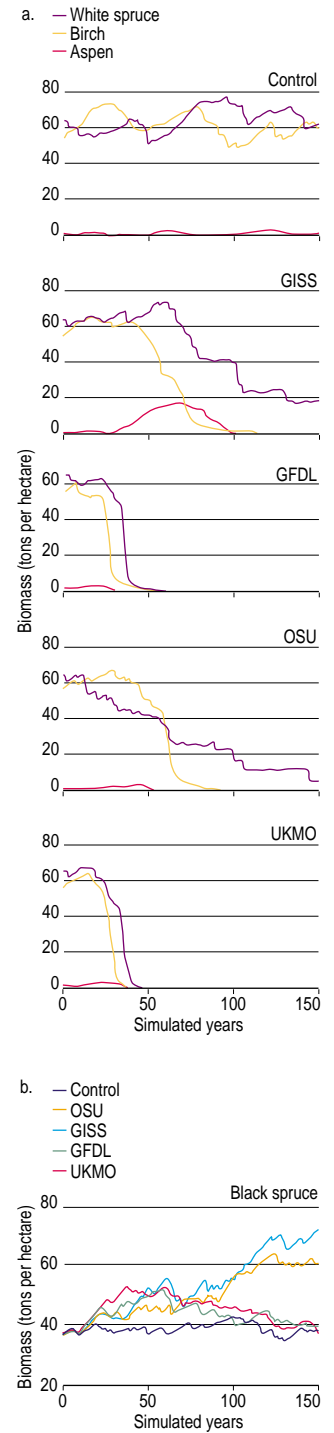
a. — White spruce — Birch — Aspen

Biomass (tons per hectare)

Simulated years

b. — Control — OSU — GISS — GFDL — UKMO

Black spruce

Biomass (tons per hectare)

Simulated years

Fig. 10. Changes in biomass from gap model simulations for central Alaska sites with a) south-facing slopes and b) north-facing slopes for present climate (control) and for different climate model simulations with doubled CO_2 (Smith et al. 1992). GISS = Goddard Institute for Space Studies, GFDL = Geophysical Fluid Dynamics Laboratory, OSU = Oregon State University, UKMO = United Kingdom Meterological Office.
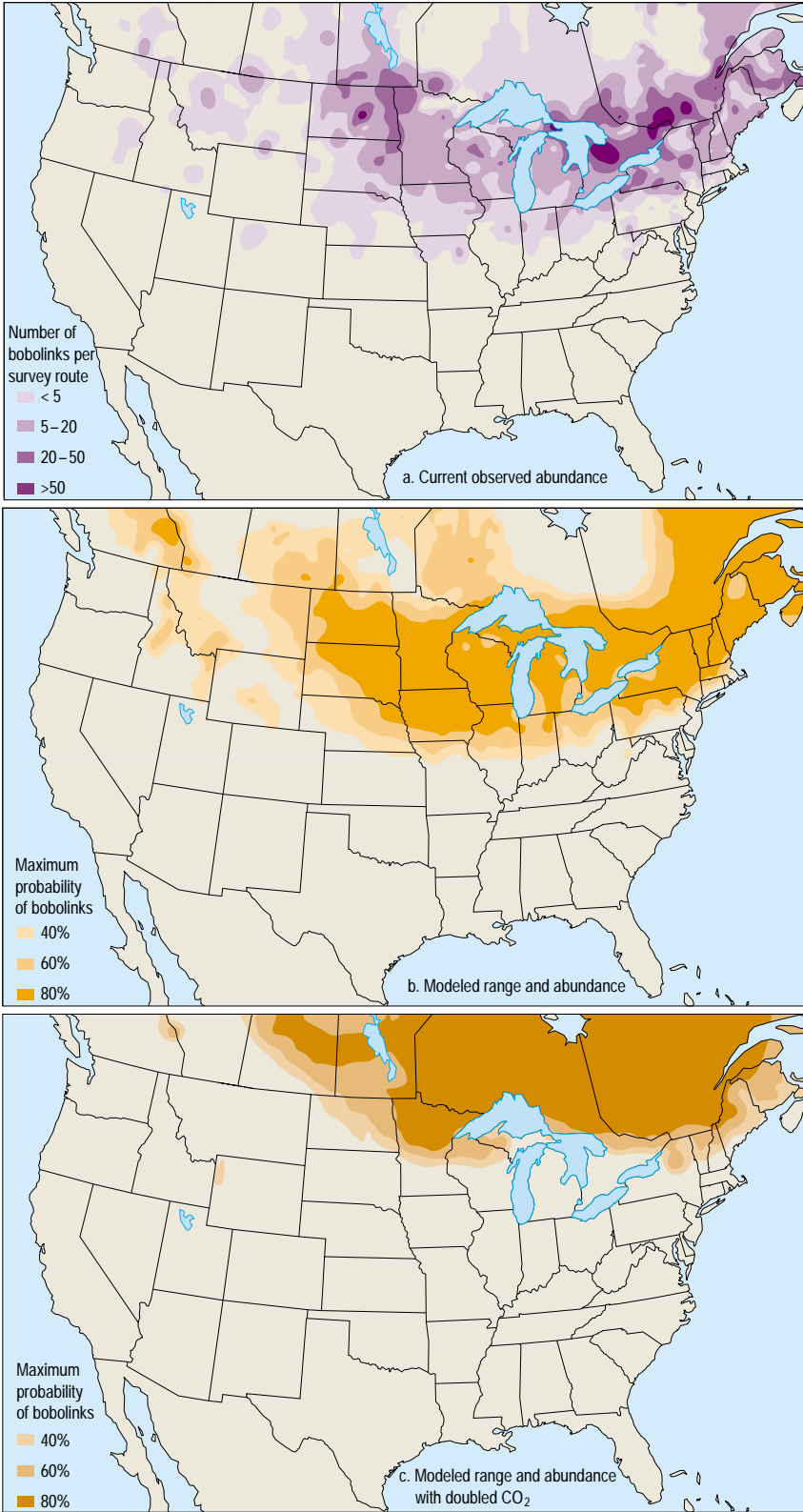
© Academic Press

Number of
bobolinks per
survey route
- < 5
- 5–20
- 20–50
- >50

a. Current observed abundance

Maximum
probability
of bobolinks
- 40%
- 60%
- 80%

b. Modeled range and abundance

Maximum
probability
of bobolinks
- 40%
- 60%
- 80%

c. Modeled range and abundance
with doubled CO_2

© J. Price

Fig. 11. a) Map of current range and abundance of the bobolink as determined from actual observations during the U.S. Geological Survey Breeding Bird Survey and b) map of current range and abundance of the bobolink as estimated from the empirical–statistical model. The high correspondence in patterns between maps a and b suggests that this model reliably captures many of the features of the actual observed range and abundance of this species as depicted in map a. c) Map of the forecasted range and abundance of the bobolink for climate change response of a model with doubled CO_2. This map illustrates the potential for very significant shifts that doubled CO_2 could cause (Price 1995).

human-induced climatic changes could occur rapidly when compared with the rate of natural climatic changes, and because the dispersal ability of most herptiles is painfully slow, even without considering the additional difficulties associated with human land-use changes disturbing their migration paths.

Several reptile species could exhibit vulnerability to climatic change because of an unusual characteristic: their sex is determined by the temperature experienced as they develop inside the egg. Such temperature-dependent sex determination makes these animals uniquely sensitive to temperature change, meaning that climatic change could potentially cause dramatic range contractions. For example, the European pond turtle, a species whose sex is determined by temperature, colonized England (Stuart 1979) and Denmark (Degerbol and Krog 1951) during a warm period in the late Ice Age. With the return of colder temperatures, these populations rapidly disappeared. Holman (1990; University Museum, Michigan State University, East Lansing, personal communication) suggested that a combination of shorter summers, which reduced available incubation time, and biased sex ratios, which were due to cooler summers, could easily have caused the swift retreat of this turtle to a more southern range.

Most North American turtles are subject to temperature-dependent sex determination (Ewert and Nelson 1991; Ewert et al. 1994); their populations can vary over the years from 100% males to 100% females (Mrosovsky and Provancha 1992; Janzen 1994). Janzen found that sex ratios were closely linked to mean July temperature, and he demonstrated that under conditions predicted by climate change models, populations of turtles will regularly produce only females within 50 years.

In general, animals most likely to be affected earliest by climatic change are those in which populations are fairly small and limited to isolated habitat islands. As a result of human-generated landscape changes, many reptiles now fall into this category, as do many other animals. Indeed, temperature-dependent sex-determined species are especially likely to suffer from extreme sex ratio biases, and therefore their sensitivity to rapid climate change appears potentially more severe than most other animals.

There are estimates that a number of small mammals living near isolated mountaintops (which are essentially habitat islands) in the Great Basin would become extinct given typical global change scenarios (MacDonald and Brown 1992; Fig. 13). Recent studies of small mammals in Yellowstone National Park show that statistically significant changes in both abundances and physical sizes of some species
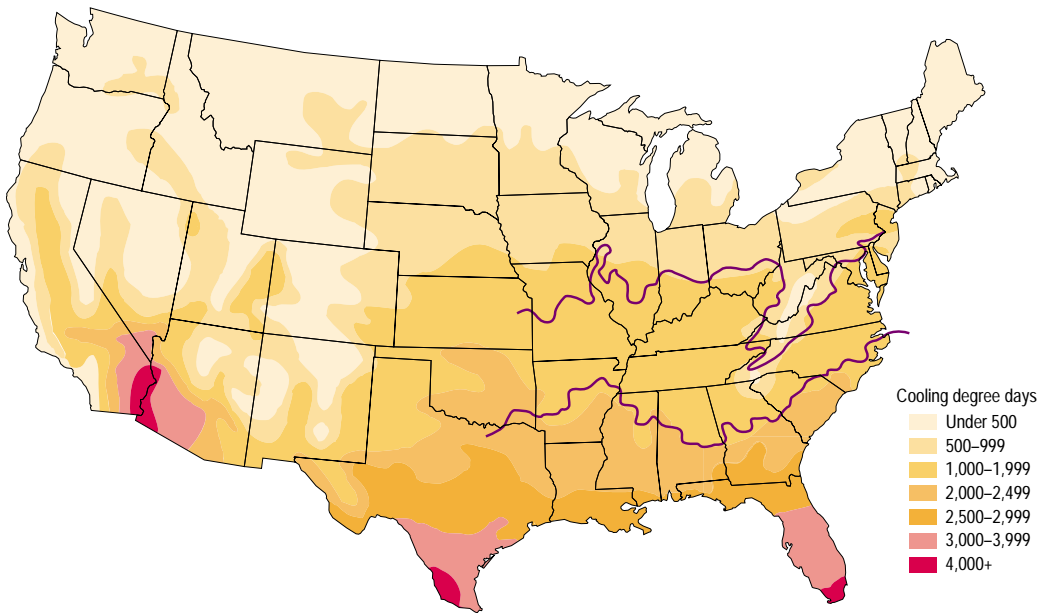
Fig. 12. Strong associations are evident between the northern range limit of the broad-headed skink (upper purple line) and 1,000 cooling degree-days, and between the northern range limit of the American alligator (lower purple line) and 2,000 cooling degree-days, suggesting the importance of climate on the large-scale biogeographic patterns of both species. Cooling degree-days indicate the accumulated number of degrees Fahrenheit over a year above a threshold of 65° F (R. L. Burke and T. Root, University of Michigan, Ann Arbor, personal communication).

occurred with historical climate variations (which were much smaller than most projected climate changes for the next century), but there appear to have been no simultaneous genetic changes (Hadley et al. 1997; E. A. Hadley, Montana State University, Bozeman, unpublished manuscript). Therefore, it is likely that climate change in the twenty-first century could cause substantial alteration to biotic communities, even in protected habitats such as Yellowstone National Park. In addition, the biomass of macrozooplankton in waters off southern California has decreased dramatically as surface waters warmed (Roemmich and McGowan 1995; Fig. 14). Similarly, a study suggests that statistically the range of the Edith's checkerspot butterfly in western North America has shifted northward and upward in association with long-term regional warming trends (Parmesan 1996).

Top-Down Approaches

The biogeographic approach just summarized is an example of a top-down technique (for example, Holdridge life-zone classification, Fig. 9), in which data on abundances or range limits of vegetation types or biomes are overlain on data of large-scale environmental factors such as temperature or precipitation. When associations among large-scale biological and climatic patterns are revealed, biogeographic rules expressing these correlations graphically or mathematically can be used to forecast changes in vegetation driven by given climate changes. Price's maps of the changes in bird ranges (Fig. 11) are also an example of such a top-down approach. As noted earlier, though, such top-down approaches are not necessarily capturing the important mechanisms responsible for the
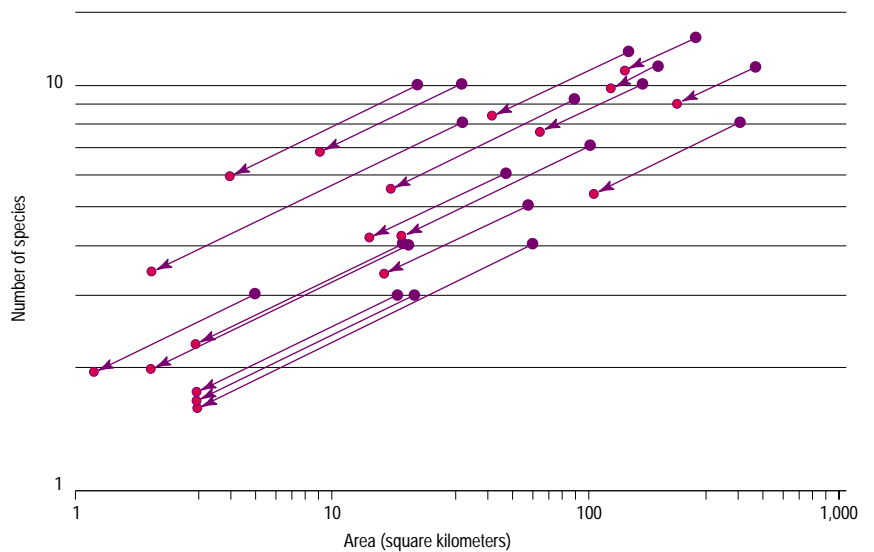

association—the association itself may be a chance occurrence. Scientists therefore strive to look at smaller scales for processes that account for the causes of biogeographic associations, in the belief that the laws discovered at smaller scales will apply at large scales as well.

Bottom-Up Approaches

The next traditional analysis and forecasting technique is often referred to as bottom-up. Small-scale ecological studies have been undertaken at the scale of a plant or even a single leaf (Idso and Kimball 1993) to understand how, for example, increased atmospheric CO_2 concentrations might directly enhance photosynthesis, net primary production, or water-use efficiency. Most such studies indicate increases in all these factors, increases that some researchers have
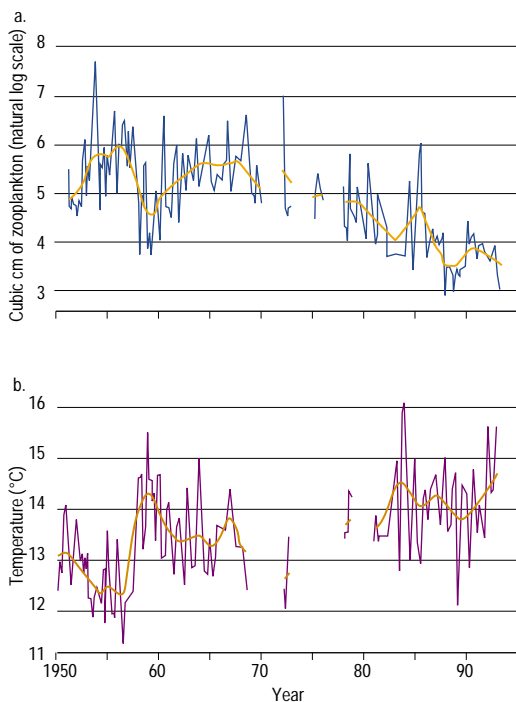
Fig. 13. Predicted changes in the number of species of small mammals inhabiting 19 isolated mountain ranges in the Great Basin after extinctions caused by (the assumed scenario of) climate and subsequent vegetation change. Such climate change would decrease the amount of suitable habitat for these species that live in island-type regions, eventually leading to a number of extinctions. For each mountain range, the purple dot represents the present number of species per square kilometer, the red dot indicates the predicted number per square kilometer after extinctions, and the arrow connecting the two points shows the magnitude of change (MacDonald and Brown 1992).

© Blackwell Science

Fig. 14. a) Time series of zooplankton volume (cubic centimeters of zooplankton per 1,000 cubic meters of seawater strained in the Southern California Bight), and b) time series of the upper 100 meters of average temperature of seawater for a). On the logarithmic scale, a change of -1.6 is the change from the mean of the 1950–1970 data to the minimum in the 1990's and is equivalent to an 80% decrease (Roemmich and McGowan 1995).

© Science

turn, would increase transpiration, thereby off-setting some of the direct CO_2/water-use efficiency improvements observed experimentally at the scale of a single leaf or plant. Regardless of the extent to which this forest-scale feedback effect will offset inferences made from bottom-up studies of isolated plants, the following general conclusion emerges: the bottom-up methods may be appropriate for some processes at some scales in environmental science, but they cannot be considered credible without some sort of validation testing at the scale of the system under study. Schneider (1979) has made the same point for climate models, as do several authors in Ehleringer and Field (1993) for vegetation modeling. Harte et al. (1995) used actual field experiments with heaters to simulate global warming as an experiment to demonstrate top-down/bottom-up connections.

Combined Top-Down and Bottom-Up Approaches

To help resolve the deficiencies of the top-down biome forest models mentioned previously, more process-based, bottom-up approaches such as forest gap models have been developed (Botkin et al. 1972; Pastor and Post 1988; Smith et al. 1992). These models include individual species and can calculate vegetation dynamics driven by time-changing climatic change scenarios. Such models typically assume a random distribution of seed germination in which juvenile trees of various species appear. Whether these trees grow well or just barely survive depends on whether they are shaded by existing trees or grow in relatively well-lit gaps, what soil nutrients are available, and other environmental factors such as solar radiation, soil moisture, and temperature. Under ideal conditions, individual tree species are assigned a sigmoid (S-shaped) curve for growth in trunk diameter. So far, this approach may appear to be the desired process-based, bottom-up technique, an impression reinforced by the spatial scale usually assumed, about 0.1 hectares. But the actual growth rate calculated in the model for each species has usually been determined by multiplying the ideal growth rate curve by a series of growth-modifying functions that attempt to account for the limiting effects of nutrient availability, temperature stress, and so forth. These growth-modifying functions for temperature are usually determined empirically at a large scale by fitting an upside-down U-shaped curve, whose maximum is at the temperature midway between the average temperature of the species' northern range limit and the average temperature of its southern range limit (Fig. 15). Growing degree-days (related to temperature but not temperature per se) are used in this scenario.
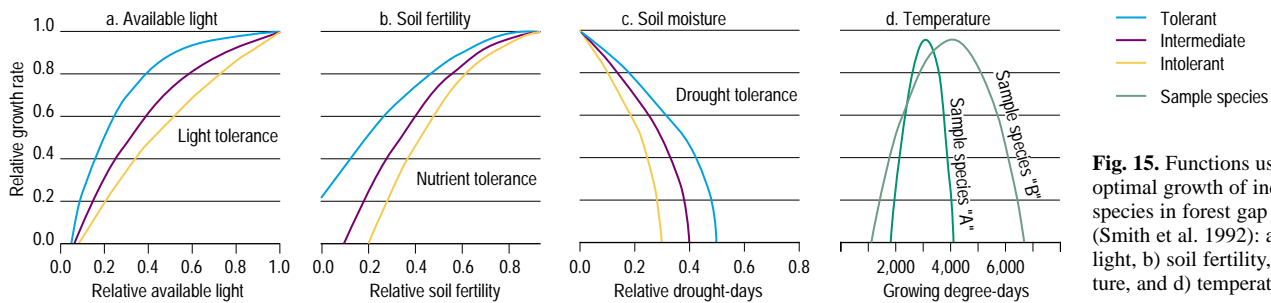
extrapolated to ecosystems (Idso and Brazel 1984; Ellsaesser 1990).

To what extent can we reasonably project from experiments that use single leaves or single plants to more complex and larger environmental systems, such as an entire tundra (Oechel et al. 1994) or forest ecosystem (Bazzaz 1990; Bazzaz and Fajer 1992)? Forest ecosystem models driven only by global climate change scenarios in which CO_2 was doubled in a global circulation model typically project dramatic alteration to the current geographic patterns of global biomes (Prentice 1992; Smith et al. 1992; Neilson 1993). But when such forest prediction models are modified to explicitly account for some of the possible physiological changes resulting from doubled CO_2, such as change in water-use efficiency, they use the empirical results from small-scale studies to extrapolate to whole forests. This bottom-up method dramatically reduces the percentage of land area predicted to experience biome change for any given climate change scenario (Vegetation/Ecosystem Modeling and Analysis Project 1995). Prentice et al. (1992), though, building on the work of McNaughton and Jarvis (1991), excluded extrapolations of the effects of direct CO_2/water-use efficiency from their model.

At the scale of a forest, the relative humidity within the canopy, which significantly influences the evapotranspiration rate, is itself regulated by the forest. In other words, if an increase in water-use efficiency decreased the transpiration from each tree, the aggregate forest effect would be to lower relative humidity. This, in

Fig. 15. Functions used to modify optimal growth of individual species in forest gap models (Smith et al. 1992): a) available light, b) soil fertility, c) soil moisture, and d) temperature.
© Academic Press

Understanding Climate Change Effects on Glacier National Park's Natural Resources

Determining past trends and the present status of biological resources is essential for effective decision making at national parks and other lands held in the public trust. Today, however, managers have a more powerful tool for making decisions—the ability to reliably forecast resource conditions under various future scenarios. This is particularly evident when considering potential effects of climatic change on national biological resources.

Although predicting the future has always been an uncertain business, with support from the U.S. Geological Survey Global Change Research Program, scientists have further developed the capability for simulating the function and structure of northern Rocky Mountain ecosystems (Fig. 1). The Regional Hydro-Ecological Simulation System (RHESSys) provides quantitative estimates of key ecosystem processes for any specified point in time or space (White and Running 1994).

A concurrently developed model, FIRE-BGC (biogeochemistry), can translate RHESSys estimates into the probable age, size, and species composition of a forest 100 years in the future on any specified mountain slope in Glacier National Park (Keane et al. 1996; Fig. 2). The predictions are spatially explicit, meaning that future forests can be calculated and mapped for each slope and aspect of the mountain landscape. The models are also mechanistic, meaning that components such as trees are "grown" in the virtua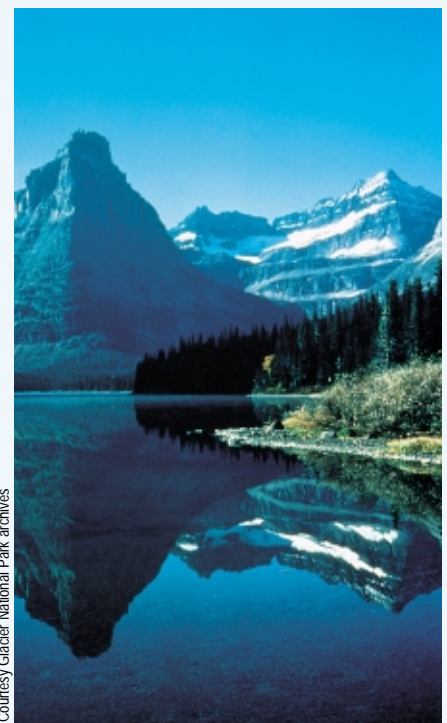l reality of computer memory by using biophysical principles and calculations, rather than by being estimated through empirical means. Finally, future landscapes can be generated by using various projections of future climates. These climatic scenarios can be imported to RHESSys from larger-scale climate modeling efforts.

RHESSys does not predict future climates; instead, it translates projected climate scenarios into tangible ecological changes on landscapes at Glacier National Park. Because RHESSys is spatially explicit in describing future conditions and can be displayed on a computer monitor or map, it can convey a powerfully intuitive understanding of potential landscape changes.
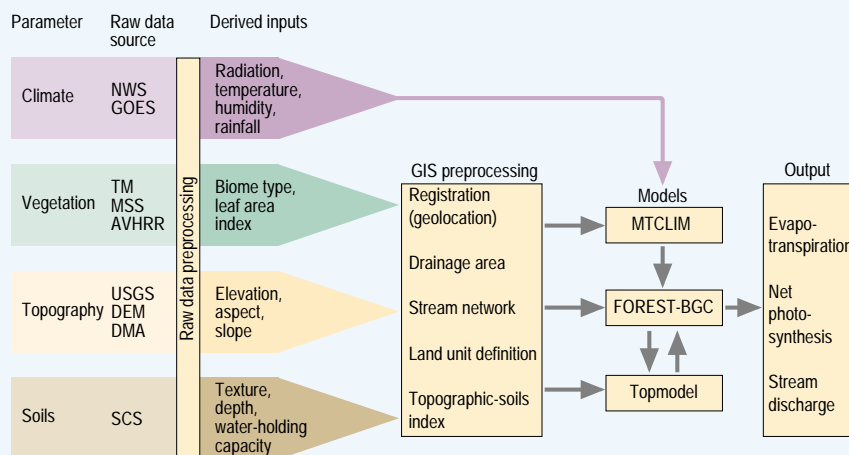
Sources:
NWS: National Weather Service
GOES: Geostationary Operational Environmental Satellite
TM: Landsat/Thematic Mapper
MSS: Landsat/Multispectral Scanner
AVHRR: NOAA/Advanced Very High Resolution Radiometer
USGS: U.S. Geological Survey
DEM: Digital Elevation Model
DMA: Defense Mapping Agency
SCS: Soil Conservation Service

Models:
MTCLIM: mountain microclimate simlulator
FOREST-BGC: forest ecosystem simulator
Topmodel: hydrological routing simulator

© Journal of Vegetation Science

Fig. 1. RHESSys, the Regional Hydro-Ecological Simulation System, integrates data from various standard sources into a series of interacting models that provide quantitative estimates of ecosystem functions (modified from White and Running 1994).

Courtesy Glacier National Park archives

Fig. 2. Glacier National Park encompasses a 4,078 square-kilometer forested, mountainous landscape with numerous alpine lakes and streams.

How Modeling Works

RHESSys uses remotely sensed imagery and other satellite data to provide the geographic distribution of vegetation cover types for Glacier National Park. By combining this information with elevation data in a geographic information system (GIS), the computer can create a three-dimensional digital landscape. Estimates of biomass or rates of photosynthetic activity for each vegetation cover type in the park are made from satellite data by using other tested techniques (Running et al. 1989). RHESSys then "knows" approximately what is on the landscape and where it is; next it needs to estimate landscape response to environmental changes.

A microclimate model (MTCLIM) takes daily meteorological measurements and, by using mathematical expressions of physical principles, extrapolates those data to every point in the mountainous terrain (Hungerford et al. 1989). Thus, the daily changes in microclimate experienced by each stand of trees in the park is calculated. A forest biogeochemistry model (FOREST-BGC) uses the microclimate calculations (such as relative humidity or solar radiation) and appropriate biophysical principles to estimate daily tree response (Running and Gower 1991). The net result is that RHESSys can simulate forest ecosystem processes daily for many years and across large areas of Glacier National Park.

Of course, tree growth is determined by more than just daily weather, which is why the various models within RHESSys interact. For instance, the responses of a forest stand to changes in microclimate are passed along to calculate the effects of increasing tree growth on soil moisture. Reductions in soil moisture provide feedback to another model, which estimates streamflow in each forested drainage. Changes in soil moisture also provide feedback to the model, which estimates rates of tree growth and so on. An advantage to the RHESSys structure is that the individual models can be tested and improved independently without changing the entire simulation system. This allows RHESSys to quickly take advantage of continuing improvements in ecological modeling.

RHESSys estimates ecological processes such as rates of evapotranspiration, hydrological balance, or net primary productivity (Fig. 1). FIRE-BGC is a biogeochemical succession model that uses those estimates to generate the physical structure and species diversity of forests. FIRE-BGC defines homogeneous landscape units (like forest stands) and calculates individual tree growth, death rates, seedling survival, organic matter accumulation, and
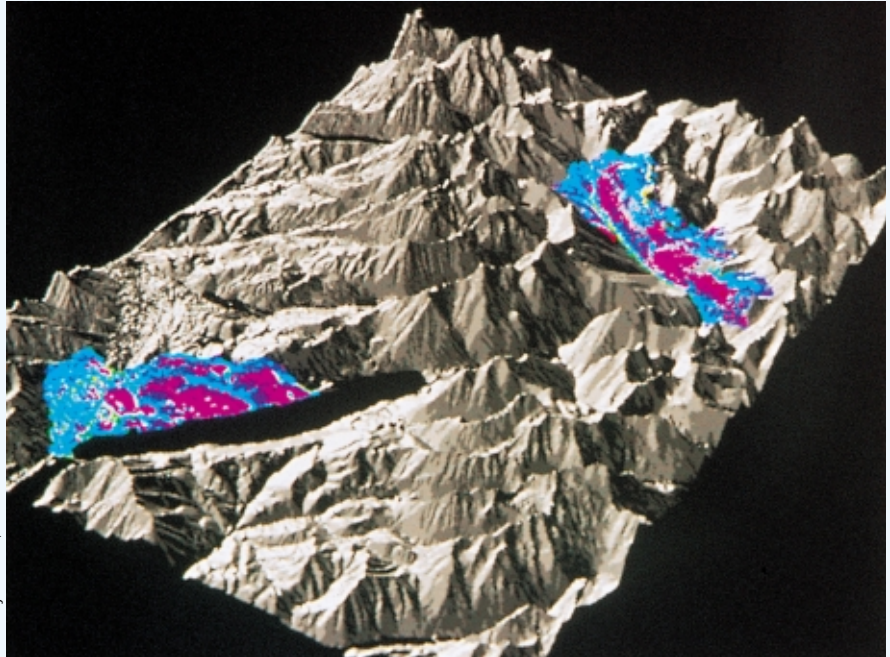

Courtesy R. Keane, U.S. Forest Service

Fig. 3. A forest succession model, FIRE-BGC, predicts the occurrence of two major forest fires in the upper McDonald watershed during simulation year 163. Blue colors are the cooler part of the fire, pink the hottest parts. The boundaries and intensity of the potential future fire are calculated by another model, FARSITE, based on such parameters as fuel loads and simulated daily meteorology.

decomposition both daily and annually. The replacement of one stand of trees by another stand (succession) can be tracked through time as tree demographic processes take place. The role of ecological disturbances, such as large forest fires, has also been integrated (Finney and Ryan 1995; Fig. 3).

How Well Do the Models Work?

We can test model performance by comparing ecosystem processes simulated for present conditions with measurements of the real ecosystem. Climate data for Glacier National Park's Lake McDonald basin have been used to drive a RHESSys simulation for the same period when numerous field measurements were being taken. For instance, thousands of snow depth measurements were made to verify the RHESSys estimates of snowpack distribution and moisture content. This test was critical because snowpack provides significant moisture during summer months for many ecosystem functions. Automated weather stations were placed on remote mountain slopes to confirm that the microclimate model was making reasonable predictions of climatic variables (Fig. 4). Many other ecosystem measurements were taken, including stream discharge volume and timing. Figure 5 shows the relation between the streamflow that actually occurred and what

Courtesy F. Klasner, USGS

Fig. 4. Research scientists from the U.S. Geological Survey and National Park Service at an automated climate station above Lake McDonald, Glacier National Park. Data collected from this station will help verify the meteorological estimates generated by a submodel of RHESSys.

RHESSys predicted would occur (Comanor et al. 1997). Other comparisons of modeled and measured ecosystem phenomena showed similar relationships.

RHESSys is able to reasonably simulate the underlying dynamics that drive ecological changes in Lake McDonald basin. These
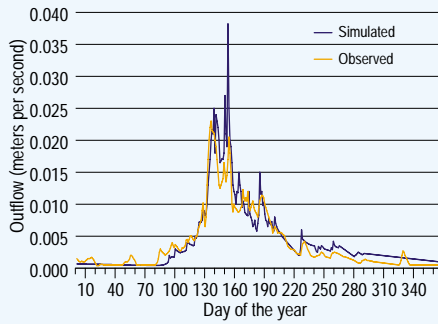
Fig. 5. A comparison of the observed and simulated outflow (meters per second) from the upper Lake McDonald watershed, Glacier National Park, 1993. Simulated outflows were calculated by RHESSys.

© J. White, University of Montana

Fig. 6. Estimated changes in vegetation cover by 2050 for the Lake McDonald watershed, Glacier National Park, following climate change. Changes were estimated by RHESSys by using a climate change scenario of a 30% increase in annual precipitation and a 0.5°C increase in average annual temperature.

simulations indicate that the Glacier National Park landscape is dynamic and will change over time even with a stable climate. We cannot assume, however, that the climate is not changing.

Predicting Climate Change Effects

Forecasting future climates is both difficult and controversial. The value of models like RHESSys is that a variety of climate scenarios can be used to simulate the range of outcomes for Glacier National Park. As climate models improve, RHESSys can use the new forecasts to identify increasingly probable ecosystem changes.

The simulation for the Lake McDonald basin in Figure 6 is based on the assumption that the regional climate will be 0.5°C warmer and will have a 30% increase in annual precipitation 50 years from now. Predicted changes in vegetation include expanded cedar–hemlock forests, making Glacier National Park resemble the wetter forests of the Pacific Northwest. A different climate scenario suggests Glacier National Park stream temperatures will rise, especially in late summer, because of changes in streamflow timing and volume. Such changes would affect temperature-sensitive aquatic organisms; for example, different species live in each section of stream as the water becomes colder with increasing elevation. Predictable shifts of these organisms upstream and to higher elevations will occur under the RHESSys-projected changes.

RHESSys accurately predicted snowfall distribution at Glacier National Park, identifying areas where snow never melted completely before the onset of the next winter. These are the same areas that currently support glaciers (White and White 1994). These glaciers have been steadily receding during this century (Fig. 7), and RHESSys
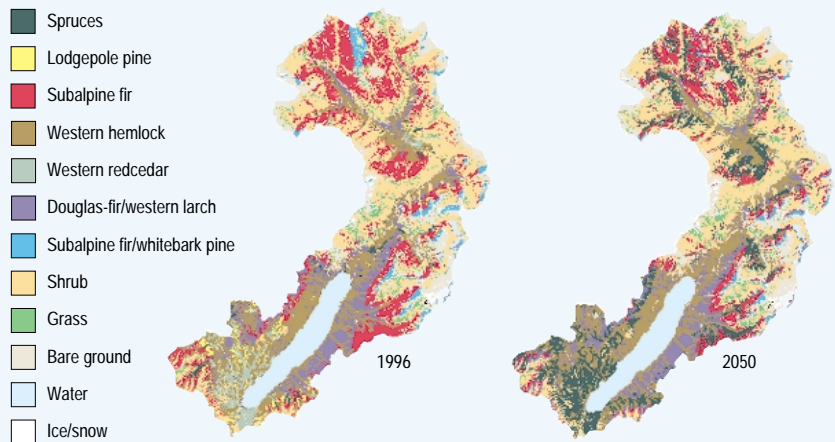

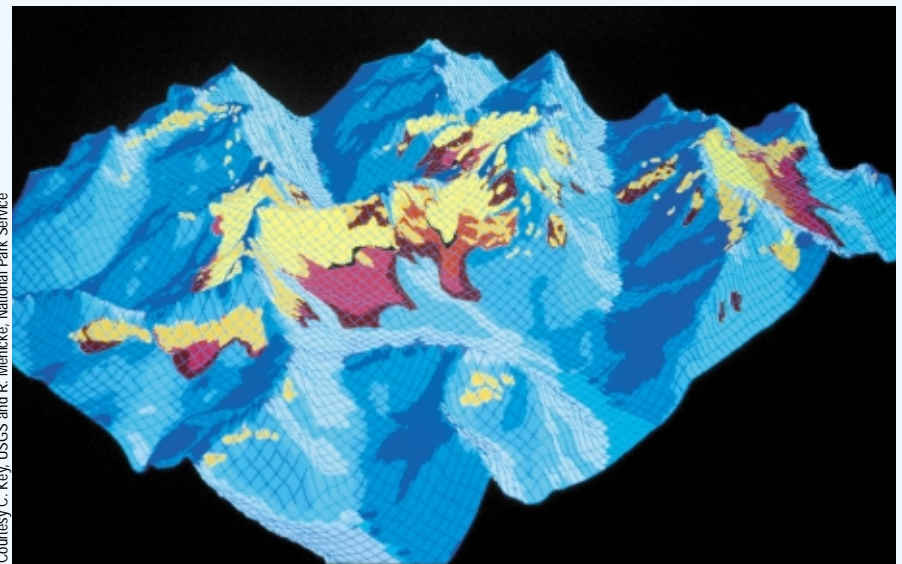Courtesy C. Key, USGS and R. Menicke, National Park Service

Fig. 7. A geographic information system representation of glacier shrinkage from 1850 to 1993 in Glacier National Park. The Blackfeet–Jackson glaciers are in the center. The yellow areas reflect the current area of each glacier; other colors represent the extent of the glaciers at various times in the past.

suggests that future snowpacks will not survive through summer to nourish glaciers. A separate modeling effort extrapolated glacial melt rates into the future by using different scenarios for global warming (Hall 1994). In this model, whether current warming trends continue or are accelerated by increasing atmospheric carbon dioxide, glaciers will not exist in Glacier National Park by 2030.

Future Models

Ecosystem modeling systematically organizes our current ecological knowledge to provide quantitative estimates we can test in the field. Once underlying ecological principles have been affirmed in the model by successful field tests, we can use a model to glimpse the future and help prepare for it.

Like climate change models, simulation systems like RHESSys and FIRE-BGC will be continually improved. It seems clear, however, that these ecosystem models will challenge us to think more specifically about the effects of climate change and will be an essential tool for understanding the future status and trends of our biological resources.

See end of chapter for references

Author

Daniel B. Fagre
U.S. Geological Survey
Biological Resources Division
Glacier Field Station Science Center
Glacier National Park
West Glacier, Montana 59936

In essence, this technique combines large-scale, top-down empirical pattern correlations into an otherwise mechanistic bottom-up modeling approach. Although this combined technique refines both approaches, it has been criticized because such large-scale, top-down inclusions are not based on the physiology of individual species and lead to confusion about the fundamental and realized niches (Pacala and Hurtt 1993). (The fundamental niche is the ecological space in which a given species could theoretically survive—for example, if its competitors were absent—and the realized niche is where it actually exists.) The question then is: what limits the realized niche, particularly at the southern boundary? Further, more refined models should include factors such as seed dispersal, so that plant recruitment is related to the preexisting population and is not simply the result of a random number generator in the computer code.

Studies of More Refined Approaches

As noted, problems with the singular use of either top-down or bottom-up methods have led to well-known criticisms. For bottom-up models, the primary problem is that some of the most conspicuous processes observable at the smaller scales may not be the dominant processes that generate large-scale patterns. The mechanisms that create larger-scale responses can be easily obscured by noisy (for example, random or unrelated) local variations, often leading to an inability to detect at small scales a coherent pattern of associations (that is, mechanisms) among variables needed for ecological impact assessments at large scales. As Dawson and Chapin (1993:318) noted, too much "information about detailed mechanisms may be inefficient, incorporating excessive detail and ignoring other aspects that are critical to understanding processes at the higher levels."

Top-down approaches suffer because of the possibility that the discovered associations at large scales are statistical artifacts that do not, even implicitly, reflect the causal mechanisms needed for reliable forecasting. As Jarvis (1993:121) stated, "A major disadvantage of a top-down model is that predictions cannot be made safely outside the range of the variables encountered in the derivation of the lumped parameter function."

A search of the literature (Wright et al. 1993; Root 1994; Harte et al. 1995) provides examples of a refined approach to analyzing across large and small scales, which Root and Schneider (1995) labeled strategic cyclical scaling. This method builds upon the combined techniques in which top-down and bottom-up approaches are applied cyclically in a strategic design that addresses a practical problem: in our context, the ecological consequences of global climatic change. Large-scale associations are used to focus small-scale investigations; this helps ensure that tested causal mechanisms are generating the large-scale relations. Such mechanisms become the laws that allow more credible forecasts of the consequences of global change disturbances. "Although it is well understood that correlations are no substitute for mechanistic understanding of relationships," Levin (1993:14) observed, "correlations can play an invaluable role in suggesting candidate mechanisms for (small-scale) investigation." Strategic cyclical scaling, however, is not only intended as a two-step process, but also as a continuous cycling process between large- and small-scale studies, with each successive investigation building on previous insights from all scales. This approach is designed to enhance the credibility of the overall assessment process (see also Vitousek 1993 and Harte and Shaw 1995), which is why strategic is the first word in strategic cyclical scaling.

If the rate at which humans are injecting greenhouse gases into the atmosphere is not greatly decreased, there is a significant chance that the Earth's climate will warm by several degrees Celsius by the year 2050 (Titus and Narayanan 1995). With that in mind, Root (1988a) examined the biogeographic patterns of all wintering North American birds. She chose this group of species because birds are important parts of ecosystems and because of the availability of the necessary data—large-scale abundance data requires a veritable small army of census takers. The National Audubon Society and the U.S. Geological Survey have such volunteer forces amassed to aid in the collection of Christmas Bird Count data and Breeding Bird Survey data, respectively. By using Christmas Bird Count data, Root determined that for a large proportion of species, average distribution and abundance patterns are associated with various environmental factors (for example, northern range limits of some species apparently may be limited by average minimum January temperature; Root 1988b, 1989; Repasky 1991). Because the Christmas Bird Count and Breeding Bird Survey do not cover the Mexican or Central American portions of wintering or breeding ranges, only characteristics of the northern limits or of species that winter entirely north of the Mexican border could be considered.

The scaling question is: What mechanisms (such as competition or thermal stress) at small scales may have given rise to the large-scale associations? Root first tested the hypothesis that local physiological constraints may be causing most of the particular large-scale, temperature-range boundary associations. She used

published small-scale studies on the wintering physiology of key species to determine that about half of the songbird species wintering in North America extend their ranges no farther north than the regions where, to avoid hypothermia during winter nights, they need not increase their metabolic rates more than roughly 2.5 times their basal metabolic rate (Root 1988c). The actual physiological mechanisms generating this 2.5 rule (Diamond 1989) required further investigation at small scales.

Field and laboratory studies examining various physiological variables (for example, stored fat) are being examined on a subset of those species that seem to follow the 2.5 rule. On a large geographic scale—along a longitudinal transect running from Michigan to Alabama (Fig. 16)—Root found that the amount of stored fat may be a limiting factor. The estimated amount of available fat at dawn under extreme conditions was much lower for those individuals near the northern boundary of their range than for those in the middle of their range (Root 1991). Root embarked on a larger, regional study to determine whether the longer nights—hence, fewer hours of daylight available for foraging—or the colder temperatures in the more northerly locations are relatively more important.

In addition to the one longitudinal transect, Root incorporated a second transect that runs from Iowa to Louisiana (Fig. 16), with the field sites on each transect paired such that pairs at the same latitude (that is, sites in Michigan and Iowa, Indiana and Missouri, Tennessee and Arkansas, and Alabama and Louisiana) have the same day length. In addition, because winter minimum isotherms run at an angle to latitude in this area of the continent, Root was able to form different pairs of the sites so that temperatures were similar (that is, sites in Missouri and Michigan, Arkansas and Indiana, and Louisiana and Tennessee have roughly the same average nightly January temperature). This larger-scale design was selected based on previous small-scale studies because it allows a decoupling of

the effects of day length and minimum temperature, which is important to the strategic problem of determining whether scenarios of global warming might have a large effect. Preliminary results indicate that changing temperatures are more likely than day length to explain this effect (Root, unpublished data). Thus, global temperature changes would probably cause a rapid range and abundance shift, at least by selected bird species. Indeed, Root found significant year-to-year shifts in ranges and abundances; these shifts are apparently associated with year-to-year changes in winter temperatures.

This shift in year-to-year ranges and abundances observed at several field sites led to another large-scale, top-down study. Root has embarked on a continentwide examination of northern range boundaries of wintering birds, but this time is looking for year-to-year variations rather than average limits or abundances. Her first step was to quantify the year-to-year variations of selected species (Root 1994), the next to perform time-series analyses of 30 years of wintering bird abundance data and to compare these analyses with key climatic variables (for example, number of consecutive days below ¯4°C). Preliminary analysis for only one species at two sites shows that in warmer years, more individuals winter farther north than in colder years (Fig. 17). No claim is made at this point in the research for the generality of the preliminary results indicating strong and quantitative links between bird disturbances and climate. This example does permit, however, a clear demonstration of refined methods for cycling across scales to estimate ecological responses to climatic change.

A second example of refined methods—this time from a consortium of researchers rather than a single investigator—is the Cooperative Holocene Mapping Project effort referred to previously. (See Cooperative Holocene Mapping Project 1988; Wright et al. 1993; and the discussion in Root and Schneider 1995 for further details.)

Three-way Linkages Among Plants, Animals, and Climate on a Large Scale

The anticipated changes in plant ranges will probably have dramatic effects on animals, both on the large biogeographic scale and on the local regional scale. The ranges of many animals are strongly linked to vegetation. For example, red-cockaded woodpeckers are endemic to mature longleaf pine and pine–oak forests (Mengel and Jackson 1977), and the winter range of Sprague's pipit is coincident with bluestem, a grass (Root 1988a). Most
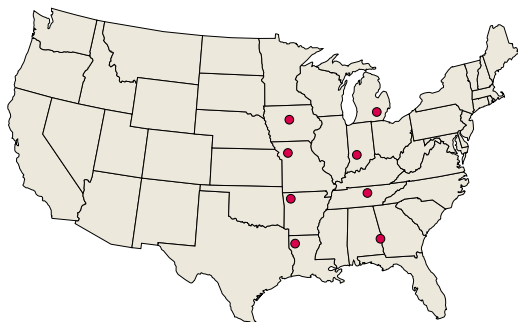

Fig. 16. Two north–south transects used to distinguish effects of day length from temperature for the northern cardinal (Root 1997).
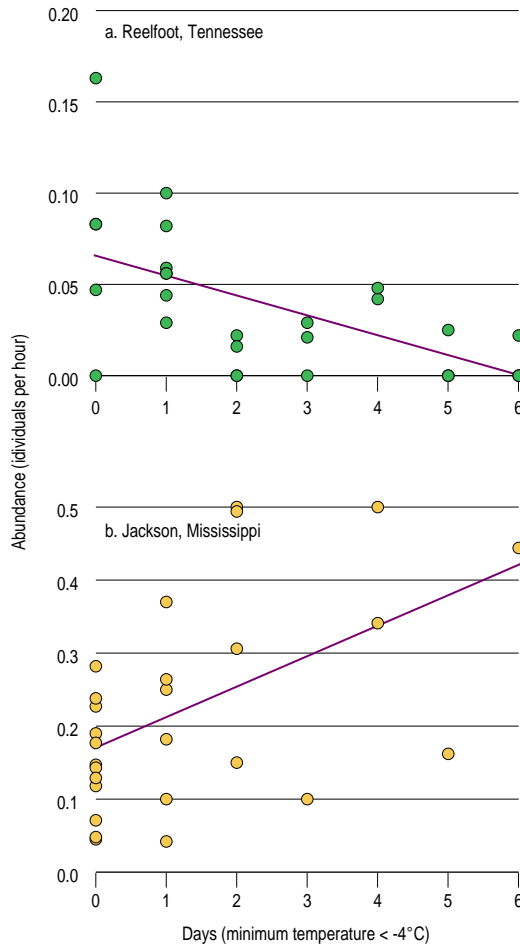
Fig. 17. The relation between annual winter abundance of the eastern phoebe from 1959–1960 to 1988–1989 and the harshness of the winter weather at two locations along the same longitudinal gradient: a) Reelfoot, Tennessee, and b) Jackson, Mississippi. In cold years, the birds move south, and in warmer years they stay farther north.

plant-eating insects are specific to plants at the generic or family level (P. A. Opler, U.S. Geological Survey, Fort Collins, Colorado, personal communication). Consequently, the ranges of various animals that rely on specific vegetation will change as the ranges of these plants shift, assuming that some other factor is not limiting them. If the climate changes more rapidly than the dispersal rates of the plants, it will result in extensive plant die-offs in the south or downslope before individuals can disperse and become established in the north or upslope. Thus, the ranges of animals relying on these plants could become compressed, and in some instances, both the plants and the animals could become extinct. For instance, the red-cockaded woodpecker needs mature, living trees for nesting sites (Jackson 1974), and if rising temperature causes most large trees to die before the newly established dispersing trees grow large enough, then this woodpecker, federally listed as endangered, could easily become extinct.

Community Disruption

Many animal species have ranges that are not directly limited by vegetation but are instead restricted by temperature. This is true for most ectotherms (insects and related arthropods, amphibians, reptiles) as well as some endotherms (mammals and birds). For example, the eastern phoebe, a North American songbird, winters in the United States in areas with average minimum temperatures warmer than -4°C (Root 1988a; Fig. 18). As the Earth warms, those species directly limited by temperature will be able to expand northward as rapidly as their dispersal mechanisms will allow, again assuming other factors are not limiting them. The animals limited by vegetation will be able to expand their ranges only as rapidly as the vegetation changes. Consequently, the potential for significant disruption among communities is high. For instance, some animals may no longer be able to coexist because an invading species disrupts the balance between competing species or between predator and prey. Therefore, to understand the ecological consequences of global climatic change on animals, the three-way linkages among animals, plants, and climate must be understood. It is critical to realize that this is not simply a one-way process whereby climate influences biota, but a three-way process, because animals and plants affect each other and are affected by climate. At the same time, altered surface vegetation can affect climate because midcontinental summer precipitation is significantly influenced by water vapor from evapotranspiration (Ye 1989; Salati and Nobre 1991).

Information Gaps

Climate Forecasts

Improve Regional Analysis, Study Transients, and Include Many Variables

The most reliable projections from climatic models are for global-scale temperature changes. Ecological impact assessments, however, need time-evolving (transient) scenarios of regional-to-local-scale climate changes. Included are changes in precipitation; severe storm intensity, frequency, and duration; drought frequency, intensity, and duration; soil moisture; frost-free days; intense heat waves; ocean currents; upwelling zones; near-ground ozone; forest canopy humidity; and ultraviolet radiation and total solar radiation reaching the surface, where photosynthesis is important. Data gathered at many scales and by coordinated volunteer and professional sources are needed for archives of these regional and local variables, which, in turn, can be used to develop and test models or other techniques for climatic forecasting.
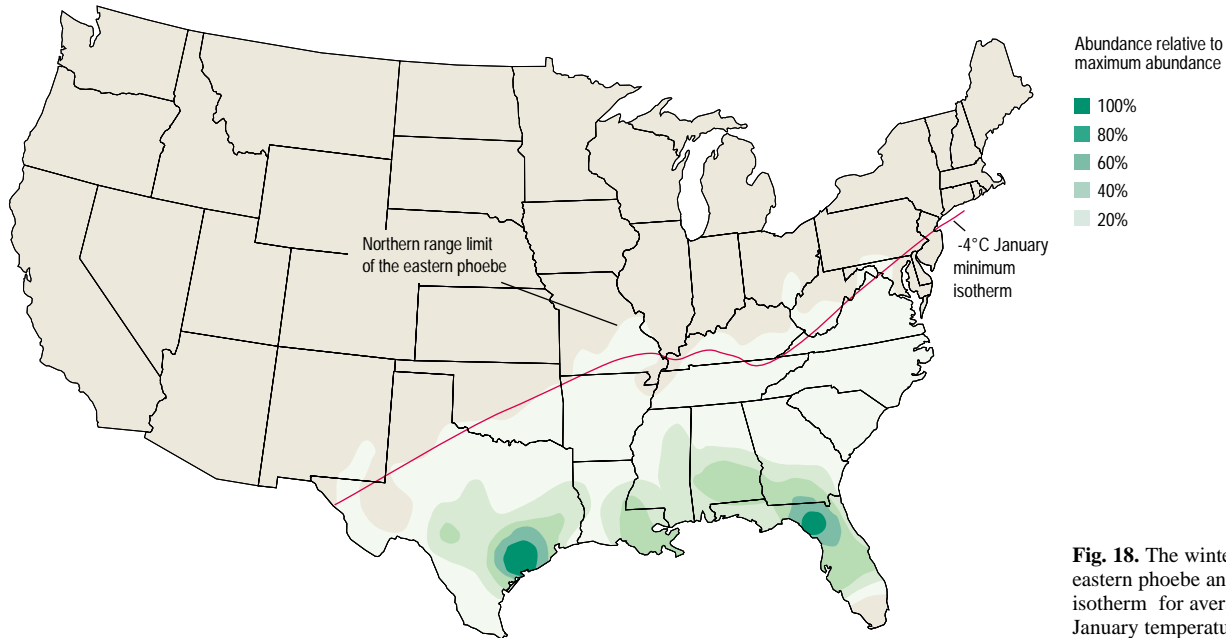
Fig. 18. The winter range of the eastern phoebe and the ‑4°C isotherm for average minimum January temperature (Root 1988b).

Abrupt Climatic Changes

We have argued that *sustained globally averaged* rates of Earth and ocean surface temperature changes from the past Ice Age to the present were about 1°C per 1,000 years. Alarmingly, this is a factor of 10 or so slower than the expected changes of several degrees Celsius per 100 years typically projected for the twenty-first century due to human effects. We emphasize the words sustained globally averaged because comparably rapid regional variations have occurred. For example, about 13,000 years ago, after warm-weather fauna had returned to northern Europe and the North Atlantic, there was a dramatic return to ice age-like conditions in less than 100 years. This Younger Dryas miniglacial lasted about 1,200 or 1,300 years before the stable recent period was established (Berger and Labeyrie 1987). The Younger Dryas was also accompanied by dramatic disturbances to plants and animals in the North Atlantic and Europe (Coope 1977; Ruddiman and McIntyre 1981). During the same period, fewer dramatic shifts occurred globally, and no significant climate change is evident in Antarctic ice cores. Even so, studies of fossils in the North Atlantic show that the warm Gulf Stream current deviated many degrees of latitude to the south and that the overall structure of deep ocean circulation may have returned to near ice age form in only decades—a weakening of the vertical circulation known as the conveyor-belt current (Broecker et al. 1985).

Plausible speculations about the cause of the Younger Dryas center on the injection of fresh meltwater into the North Atlantic, presumably associated with the breakdown of the North American ice sheet (Boyle and Weaver 1994; Paillard and Labeyrie 1994). Could such a rapid change to the conveyor-belt current be induced today by pushing the present climatic system with human disturbances such as greenhouse gases or sulfur oxides? The potential for this is speculative, of course, but its possibility has concerned many scientists (Broecker 1994).

Even more perplexing is an ice core recently drilled in Greenland; this core's record stretches back to the previous interglacial age 140,000–120,000 years ago (Greenland Icesheet Project 1993). Unlike ice in Antarctica, which tells the standard story of a relatively stable 2°C warmer interglacial period (Fig. 1), the Greenland core contains several dramatic fluctuations during the slightly warmer Eemian interglacial, equivalent to the occurrence of some 5°C changes happening within a century or less (locally, at least). Could a human-caused global warming of 2°C—expected as likely in the decades ahead (Intergovernmental Panel on Climate Change 1996a)—trigger such "surprise" climatic instabilities as may have occurred 140,000–120,000 years ago? Again, this is speculation based on a possible but unconfirmed result. Still, the prospect of climatic surprises in general is chilling enough to lend considerable urgency to the need to speed up the rate of our understanding, slow down the rates at which we are forcing nature to change, or both.

Adaptability

Our current inability to credibly predict time-evolving regional climatic changes

has many implications, one of which concerns the adaptability of agricultural ecosystems. That is, any experience farmers might have with anomalous weather in, say, the 2020's, may not help them adapt to the evolving climate change in the 2030's, because a transient climate change could differ dramatically over time. This would inhibit learning by doing, creating a potential lack of adaptability associated with the difficulty of reliably predicting regional climatic consequences (Schneider 1996). Such rapid climate changes would be especially difficult for natural ecosystems to adapt to because habitats do not have the luxury of "choosing" to plant new seeds or change irrigation systems, soil tillage practices, or other agricultural practices.

Ecological Applications-Driven Climatic Research

Regional projections of climatic changes arising from a variety of greenhouse gas and sulfur oxide emissions scenarios are essential for ecological applications. Such studies must stress the climatic variables most likely to have significant effects on biological resources. For example, extreme variability measures such as high temperature and low relative humidity are important for evaluating the risk of forest fires (Torn and Fried 1992). Identifying such variables of ecological importance and communicating this information to climate scientists require close interdisciplinary, multi-institutional, and cross-scale research efforts to ensure that combinations of variables relevant to ecological applications receive research priority by climatologists. A focus of climate research toward changing climatic variability (Mearns et al. 1984, 1990; Rind et al. 1989) might be more useful for ecological impact assessments than the current focus among climatic modelers on climatic means.

Ecosystem Responses

Interactive, Multiscale, Ecological Studies Needed

Most ecological studies project the response of one species at small scales or shifts in biomes at large scales to an equilibrium, CO_2-doubled climate model (for example the Vegetation/Ecosystem Modeling and Analysis Project 1995). What is needed for more realistic and useful ecological impact assessments is a multiscale, multispecies, multitaxa analysis driven by regionally specific, transient climatic change forecasts. The construction of ecological forecast models first requires large-scale data sets gathered locally by professional (for example, U.S. Geological Survey land-cover data sets) and volunteer (for example,

National Audubon Society Christmas Bird Count) workers. Without such data sets, virtually no credible progress is possible in determining large-scale patterns of associations among ecological and climatic variables. Small-scale studies informed by large-scale patterns are then needed to refine causal mechanisms underlying such large-scale associations, thereby testing the formulas used to make projections of various species or biome responses to hypothesized global changes. For example, Pacala and Hurtt (1993) suggested small- to medium-scale experiments to improve forest gap models. Their criticisms suggest that largely first principles, bottom-up models may still be unrealistic if some top-down parameters (that is, growth-modifying functions in the instance of gap models) are not appropriately derived from data at the scale at which the model is being applied (Root and Schneider 1995).

One obvious truism emerges: credible modeling required for forecasting across many scales and for complex interacting systems is a formidable task requiring repeated testing of many approaches. Nevertheless, tractable improvements in refining combined top-down and bottom-up techniques can be made. It will, however, take more than one cycle of interactions to reliably address the cross-scale and multicomponent problems of ecological assessment—what we (Root and Schneider 1995) have elsewhere labeled strategic cyclical scaling.

Synergistic Effects

One of the most potentially serious global change problems is the synergistic or combined effects of habitat fragmentation and climate change. People fragment natural habitats for farmland, settlements, mines, or other developmental activities (see chapter on Land Use). If climate changes, individual species of plants and animals will be forced to adjust if they can, as they have in the past. It seems unlikely that all of the migrating species that survived the Ice Age would be able to safely reach refuges after migrating across freeways, agricultural zones, industrial parks, military bases, and cities of the twenty-first century. An even further complication arises with the imposition of the direct effects of changes in CO_2, which can change terrestrial and marine primary productivity as well as alter the competitive relations among photosynthesizing organisms.

One representative instance of synergism is that of the Kirtland's warbler in northern Michigan; this species is restricted to a narrow area of jack pines that grow in sandy soil (Botkin et al. 1991). Forest gap models of growth and decline of jack pines indicate that this species will move north with warming, but

the Kirtland's warbler will not likely survive the transition. This bird nests on the ground under relatively young pines, and the soil to the north is not generally sandy enough to allow sufficient drainage for successful fledging of young (Cohn 1989). Consequently, global warming could well doom the warbler to extinction in 30–60 years. This potential for extinction indicates how the already high rate of extinctions around the world would be exacerbated by climatic changes occurring more rapidly than species can adapt (see Pimm 1991; Peters and Lovejoy 1992; Wilson 1992).

The synergism question raises a controversial management problem of anticipating global change risk and responding by setting up interconnected nature reserves to ensure against some species becoming extinct in the event of climate changes. Alternatively, we could simply let the remnants of relatively immobile wildlife and natural plant communities remain in isolated reserves and parks as now exist. If we do opt for more environmental safeguards by interconnecting our parks, the question then becomes how we interconnect the nature reserves. Priorities must be set and money made available for constructing natural corridors through which species can travel. For example, elevated sections of highways may be needed to allow for migration routes, similar to what was done for the caribou in the Arctic when the Alaskan pipeline was built.

Policy Implications

Climatic change as now envisioned is not necessarily a threat to the well-being of all climate-sensitive species. However, the transient nature of most projected human-induced climatic change scenarios suggests that significant alterations are likely on a scale of decades, whereas the adaptability of many species—especially those upon which faster responding species depend—is on a scale of centuries. These different rates of climate change and species adaptability imply that substantial disequilibrium within ecosystems could be created because of maladaptations, significant shifts in the ranges of some species, and inevitable extinctions that result from the need to migrate rapidly through fragmented habitats and areas where traditional migratory routes are

disturbed by human land-use changes. Consequently, the only outcomes that can be predicted with virtual certainty are major surprises. The only forecast that seems unassailable is that the more rapidly the climate changes and the more extensively other human disturbances are forced on nature, the higher the probability of substantial disruption and surprise within natural systems.

Dramatic disruption of communities can be expected to occur in the next century under these conditions. To forecast possible consequences of the projected climate changes, single-species studies should be guided by the overall effects that climate may have at the large scale or on range limits and abundance patterns, and on the interactions among species. Coupling such results with information from climatologists, geologists, and others will allow interdisciplinary teams to more reliably forecast the possible biological consequences of scenarios of global warming and other global changes. These forecasts can then be used by policy makers and the general public to determine what types of actions might be effective to mitigate potential impacts of forecasted climate changes. Research can help put such policy making on a firmer factual basis, but any plausible level of effort is not likely to reduce all important uncertainties before the global change experiment now under way on Earth is played out (for example, Schneider 1997). This fact lends a real sense of urgency to research and policy communities concerned about biological conservation.

Authors

Stephen H. Schneider
Department of Biological Sciences and Institute for International Studies
Stanford University
Stanford, California 94305

Terry L. Root
School of Natural Resources and Environment
University of Michigan
Ann Arbor, Michigan 48109

Cited References

Barron, J., and A. D. Hecht, editors. 1985. Historical and paleoclimatic analysis and modeling. John Wiley & Sons, New York. 445 pp.

Bazzaz, F. A. 1990. The response of natural ecosystems to the rising global CO_2 levels. Annual Review of Ecology and Systematics 21:167–196.

Bazzaz, F. A., and E. D. Fajer. 1992. Plant life in a CO_2-rich world. Scientific American 226:68–74.

Berger, W. H., and L. D. Labeyrie, editors. 1987. Abrupt climate change. D. Reidel Publishing, Dordrecht, The Netherlands. 425 pp.

Bongaarts, J. 1992. Population growth and global warming. Population and Development Review 18:299–319.

Botkin, D. B., J. R. Janak, and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60:849–872.

Botkin, D. P., D. A. Woodby, and R. A. Nisbet. 1991. Kirtland's warbler habitat: a

possible early indicator of climate warming. Biological Conservation 56:63–78.

Box, E. O. 1981. Macroclimate and plant forms: an introduction to predictive modeling in phytogeography. Junk, The Hague. 258 pp.

Boyle, E., and A. Weaver. 1994. Conveying past climates. Nature 372:41–42.

Broecker, W. S. 1994. Massive iceberg discharges as triggers for global climate change. Nature 372:421–424.

Broecker, W. S., D. M. Peteet, and D. Rind. 1985. Does the ocean-atmosphere system have more than one stable mode of operation? Nature 315:21–25.

Budyko, M. I., A. B. Ronov, and A. L. Yanshin. 1987. History of the Earth's atmosphere. Springer-Verlag, New York. 139 pp.

Charlson, R. J., J. Langner, H. Rodhe, C. B. Leovy, and S. G. Warren. 1992. Perturbation of the Northern Hemisphere and radiative balance by backscattering from anthropogenic sulfate aerosols. Tellus 43a, b:152–163.

Cohn, J. P. 1989. Gauging the biological impacts of the greenhouse effect. BioScience 39:142–146.

Coope, G. R. 1977. Fossil coleopteran assemblages as sensitive indicators of climate changes during the Devensian (last) cold stage. Proceedings of the Philosophical Transactions of the Royal Society of London B(280):313–340.

Cooperative Holocene Mapping Project. 1988. Climatic changes of the last 18,000 years: observations and model simulations. Science 241:1043–1052.

Crowley, T. 1993. Use and misuse of the geologic "analogs" concept. Pages 17–27 *in* J. A. Eddy and H. Oeschger, editors. Global changes in the perspective of the past. Dahlem Workshop Report ES12. John Wiley & Sons, Chichester, England.

Darwin, C. 1859. On the origin of species by means of natural selection. John Murray, London. 432 pp.

Davis, M. B. 1990. Climatic change and the survival of forest species. Pages 99–110 *in* G. M. Woodwell, editor. The Earth in transition: patterns and processes of biotic impoverishment. Cambridge University Press, Cambridge, England.

Davis, M. B., and C. Zabinski. 1992. Changes in geographical range resulting from greenhouse warming effects on biodiversity in forests. Pages 297–308 *in* R. L. Peters and T. E. Lovejoy, editors. Global warming and biological diversity. Yale University Press, New Haven, Conn.

Dawson, T. E., and F. S. Chapin III. 1993. Grouping plants by their form-function characteristics as an avenue for simplification in scaling between leaves and landscapes. Pages 313–319 *in* J. R. Ehleringer and C. B. Field, editors. Scaling physiological processes: leaf to globe. Academic Press, New York.

Degerbol, M., and H. Krog. 1951. Den europoiske Sumpskildpadde (*Emys orbicularis* L.) in Danmark. C. A. Reitzels Forlag, Kobenhavn. 130 pp.

Diamond, J. 1989. Species borders and metabolism. Nature 337:692–693.

Doyle, T. W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: an application of a tropical forest succession model. Pages 56–73 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession: concepts and applications. Springer-Verlag, New York.

Eddy, J. A., and H. Oeschger, editors. 1993. Global changes in the perspective of the past. John Wiley & Sons, New York. 383 pp.

Ehleringer, J. R., and C. B. Field, editors. 1993. Scaling physiological processes: leaf to globe. Academic Press, New York. 388 pp.

Ellsaesser, H. W. 1990. A different view of the climatic effect of CO_2—updated. Atmósfera 3:3–29.

Emanuel, K. A. 1987. The dependence of hurricane intensity on climate. Nature 326:483–485.

Ewert, M. A., D. R. Jackson, and C. E. Nelson. 1994. Patterns of temperature-dependent sex determination in turtles. Journal of Experimental Zoology 270:3–15.

Ewert, M. A., and C. E. Nelson. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia 1991:50–69.

Gates, W. L. 1985. The use of general circulation models in the analysis of the ecosystem impacts of climatic change. Climatic Change 7:267–284.

Giorgi, F. 1990. Simulation of regional climate using a limited area model nested in a general circulation model. Journal of Climate 3:941–963.

Graham, R. W. 1992. Late Pleistocene faunal changes as a guide to understanding effects of greenhouse warming on the mammalian fauna of North America. Pages 76–87 *in* R. L. Peters and T. E. Lovejoy, editors. Global warming and biological diversity. Yale University Press, New Haven, Conn.

Graham, R. W., and E. C. Grimm. 1990. Effects of global climate change on the patterns of terrestrial biological communities. Trends in Ecology and Evolution 5:289–292.

Graham, R. W., and J. I. Mead. 1987. Environmental fluctuations and evolution of mammalian faunas during the last deglaciation in North America. Pages 371–402 *in* W. F. Ruddiman and H. E. Wright, editors. North America and adjacent oceans during the last deglaciation. Volume K-3. Geological Society of America, Boulder, Colo.

Greenland Icesheet Project. 1993. Climate instability during the last interglacial period recorded in the GRIP ice core. Nature 364:203–207.

Hadley, E. A. 1997. Evolutionary and ecological response of pocket gophers (*Thomomys talpoides*) to late-Holocene climate change. Biological Journal of the Linnean Society 60:277–296.

Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. Science 267:876–880.

Harte, J., M. Torn, F. R. Chang, B. Feifarek, A. Kinzig, R. Shaw, and K. Shen. 1995. Global warming and soil microclimate: results from a meadow-warming experiment. Ecological Applications 5:132–150.

Henderson-Sellers, A., Z. L. Yang, and R. E. Dickinson. 1993. The project for intercomparison of land-surface parameterization schemes. Bulletin of the American Meteorological Society 74:1335–1349.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica. 206 pp.

Holman, J. A. 1990. Vertebrates from the Harper site and rapid climate warming in mid-Holocene Michigan. Michigan Academician 22:205–217.

Idso, S. B., and A. J. Brazel. 1984. Rising atmospheric carbon dioxide concentrations may increase streamflow. Nature 312:51–53.

Idso, S. B., and B. A. Kimball. 1993. Tree growth in carbon dioxide enriched air and its implications for global carbon cycling and maximum levels of atmospheric CO_2. Global Biogeochemcal Cycle 7:537–555.

Imbrie, J., A. Berger, and N. J. Shackleton. 1993. Role of orbital forcing: a two-million-year perspective. Pages 263–277 *in* J. A. Eddy and H. Oeschger, editors. Global changes in the perspective of the past. John Wiley & Sons, New York.

Intergovernmental Panel on Climate Change. 1990. J. T. Houghton, G. J. Jenkins, and J. J. Ephraums, editors. Climate change: the IPCC scientific assessment. Cambridge University Press, Cambridge, England. 364 pp.

Intergovernmental Panel on Climate Change. 1996a. J. T. Houghton, L. G. Meira Filho, B. A. Callander, N. Harris, A. Kattenberg, and K. Maskell, editors. Climate change 1995—the science of climate change. The second assessment report of the IPCC: contribution of working group I. Cambridge University Press, Cambridge, England. 572 pp.

Intergovernmental Panel on Climate Change. 1996b. R. T. Watson, M. C. Zinyowera, and R. H. Moss, editors. Climate change 1995—impacts, adaptations and mitigation of climate change: scientific technical analysis. The second assessment report of the IPCC: contribution of working group II. Cambridge University Press, Cambridge, England. 878 pp.

Intergovernmental Panel on Climate Change. 1996c. J. Bruce, H. Lee, and E. Haites, editors. Climate change 1995—economic and social dimensions of climate change. The second assessment report of the IPCC: contribution of working group III. Cambridge University Press, Cambridge, England. 448 pp.

Jackson, J. A. 1974. Gray rat snakes versus red-cockaded woodpeckers: predator–prey adaptation. Auk 91:342–347.

Jager, J., and W. W. Kellogg. 1983. Anomalies in temperature and rainfall

during warm arctic seasons. Climatic Change 5:39–60.

Janzen, F. J. 1994. Climate change and temperature-dependent sex determination in reptiles. Proceedings of the National Academy of Sciences, U.S.A. 91:7487–7490.

Jarvis, P. G. 1993. Prospects for bottom-up models. Pages 117–126 *in* J. R. Ehleringer and C. B. Field, editors. Scaling physiological processes: leaf to globe. Academic Press, New York.

Johansson, T. B., H. Kelly, A. K. N. Reddy, and R. H. Williams, editors. 1993. Renewable energy: sources for fuels and electricity. Island Press, Washington, D.C. 1160 pp.

Karl, T. R., R. W. Knight, D. R. Easterling, and R. G. Quayle. 1995. Trends in U.S. climate during the twentieth century. Consequences 1:3–12.

Kasting, J. F., O. B. Toon, and J. B. Pollack. 1988. How climate evolved on the terrestrial planets. Scientific American 258:90.

Kaufman, Y. J., R. S. Fraser, and R. L. Mahoney. 1993. Fossil fuel and biomass burning effect on climate—heating or cooling? Journal of Climate 4:578–588.

Levin, S. A. 1993. Concepts of scale at the local level. Pages 7–19 *in* J. R. Ehleringer and C. B. Field, editors. Scaling physiological processes: leaf to globe. Academic Press, New York.

Lorius, C., J. Jouzel, D. Raynaud, J. Hansen, and H. Le Treut. 1990. The ice-core record: climate sensitivity and future greenhouse warming. Nature 347:139–145.

Lough, J. M., T. M. L. Wigley, and J. P. Palutikof. 1983. Climate and climate impact scenarios for Europe in a warmer world. Journal of Climate and Applied Meteorology 22:1673.

MacDonald, K. A., and J. H. Brown. 1992. Using montane mammals to model extinctions due to global change. Conservation Biology 6:409–425.

Manabe, S., and R. J. Stouffer. 1980. Sensitivity of a global climate model to an increase of CO_2 concentration in the atmosphere. Journal of Geophysical Research 85:5529–5554.

McNaughton, K. G., and P. G. Jarvis. 1991. Effects of spatial scale on stomatal control of transpiration. Agricultural and Forest Meteorology. 54:279–301.

Mearns, L.O. 1997. Transforming the results of the climate models to the scales of impact. Intergovernmental Panel on Climate Change workshop on regional climate change for projections for impact assessment, 24–26 September. 1996, Imperial College, London. Intergovernmental Panel on Climate Change, London. In press.

Mearns, L. O., R. W. Katz, and S. H. Schneider. 1984. Extreme high temperature events: changes in their probabilities and changes in mean temperature. Journal of Climate and Applied Meterology 23:1601–1613.

Mearns, L. O., S. H. Schneider, S. L. Thompson, and L. McDaniel. 1990. Analysis of climate variability in general

circulation models: compared with observations and changes in variability in 2 × CO_2 experiments. Geophysical Research 95:20469–20490.

Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore III, C. J. Vörösmarty, and A. L. Schloss. 1993. Global climate change and terrestrial net primary production. Nature 363:234–240.

Mengel, R. M., and J. A. Jackson. 1977. Geographic variation of the red-cockaded woodpecker. Condor 79:349–355.

Morgan, M. G., and D. W. Keith. 1995. Subjective judgments by climate experts. Environmental Science and Technology 29:468A–477A.

Mrosovsky, N., and J. Provancha. 1992. Sex ratio of hatchling loggerhead sea turtles: data and estimates from a 5-year study. Canadian Journal of Zoology 70:530–538.

Neilson, R. P. 1993. Transient ecotone response to climatic change: some conceptual and modelling approaches. Ecological Applications 3:385–395.

O'Brien, S. T., B. P. Hayden, and H. H. Shugart. 1992. Global climate change, hurricanes, and a tropical rain forest. Climatic Change 22:175–190.

Oechel, W. C., S. Cowles, N. Grulke, S. J. Hastings, B. Lawrence, T. Prudhomme, G. Riechers, B. Strain, D. Tissue, and G. Vourlitis. 1994. Transient nature of CO_2 fertilization in Arctic tundra. Nature 371:500–503.

Overpeck, J. T., R. S. Webb, and T. Webb III. 1992. Mapping eastern North American vegetation change over the past 18,000 years: no analogs and the future. Geology 20:1071–1074.

Pacala, S. W., and G. C. Hurtt. 1993. Terrestrial vegetation and climate change: integrating models and experiments. Pages 57–74 *in* P. Kareiva, J. Kingsolver, and R. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Mass.

Paillard, D., and L. Labeyrie. 1994. Role of the thermohaline circulation in the abrupt warming after Heinrich events. Nature 372:162–164.

Parmesan, C. 1996. Climate and species' range. Nature 382:765–766.

Parry, M. L., and T. R. Carter. 1985. The effect of climatic variations on agricultural risk. Climatic Change 7:95–110.

Pastor, J., and W. M. Post. 1988. Response of northern forests to CO_2-induced climate change. Nature 334:55–58.

Peters, R. L., and T. E. Lovejoy, editors. 1992. Global warming and biological diversity. Yale University Press, New Haven, Conn. 386 pp.

Pimm, S. 1991. The balance of nature. University of Chicago Press, Chicago, Ill. 434 pp.

Pittock, A. B., and J. Salinger. 1982. Towards regional scenarios for a CO_2-warmed Earth. Climatic Change 4:23–40.

Prentice, I. C. 1992. Climate change and long-term vegetation dynamics. Pages 293–339 *in* D. C. Glenn-Lewin, R. A. Peet, and T. Veblen, editors. Plant

succession: theory and prediction. Chapman & Hall, New York.

Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19:117–134.

Price, J. 1995. Potential impacts of global climate change on the summer distribution of some North American grasslands birds. Ph.D. dissertation, Wayne State University, Detroit, Mich. 540 pp.

Raval, A., and V. Ramanathan. 1989. Observational determination of the greenhouse effect. Nature 342:758.

Repasky, R. R. 1991. Temperature and the northern distributions of wintering birds. Ecology 72:2274–2285.

Rind, D., R. Goldberg, and R. Ruedy. 1989. Change in climate variability in the 21st century. Climatic Change 14:5–37.

Roemmich, D., and J. McGowan. 1995. Climatic warming and the decline of zooplankton in the California current. Science 267:1324–1326.

Root, T. L. 1988a. Atlas of wintering North American birds. University of Chicago Press, Ill. 312 pp.

Root, T. L. 1988b. Environmental factors associated with avian distributional boundaries. Journal of Biogeography 15:489–505.

Root, T. L. 1988c. Energy constraints on avian distributions and abundances. Ecology 69:330–339.

Root, T. L. 1989. Energy constraints on avian distributions: a reply to Castro. Ecology 70:1183–1185.

Root, T. L. 1991. Positive correlation between range size and body size: a possible mechanism. Proceedings of the 20th International Ornithological Congress 2:817–825.

Root, T. L. 1994. Scientific/philosophical challenges of global change research: a case study of climatic changes on birds. Proceedings of the American Philosophical Society 138:377–384.

Root, T. L. 1997. Ecology: possible consequences of rapid global change. *In* G. Ernst, editor. Earth systems. Cambridge University Press, Cambridge, England. In press.

Root, T. L., and S. H. Schneider. 1993. Can large-scale climatic models be linked with multi-scale ecological studies? Conservation Biology 7:256–270.

Root, T. L., and S. H. Schneider. 1995. Ecology and climate: research strategies and implications. Science 269:334–341.

Ruddiman, W. F., and A. McIntyre. 1981. The North Atlantic Ocean during the last deglaciation. Paleogeography, Paleoclimatology, Paleoecology 35:145–214.

Salati, E., and C. A. Nobre. 1991. Possible climatic impacts of tropical deforestation. Climatic Change 19:177–196.

Santer, B. D., K. E. Taylor, T. M. L. Wigley, P. D. Jones, D. J. Karoly, J. F. B. Mitchell, A. H. Oort, J. E. Penner, V. Ramaswamy, M. D. Schwarzkopf, R. J. Stouffer, and S. F. B. Tett. 1996. A search for human

influences on the thermal structure of the atmosphere. Nature 382: 39-46

Schneider, S. H. 1979. Verification of parameterization in climate modeling. Pages 728–751 *in* W. L. Gates, editor. Report of the JOC study conference on climate models: performance, intercomparison and sensitivity studies. World Meteorological Organization–International Council of Scientific Unions.

Schneider, S. H. 1984. On the empirical verification of model-predicted CO_2-induced climatic effects. Pages 187–201 *in* J. Hansen and T. Takahashi, editors. Climate processes and climate sensitivity. American Geophysical Union, Washington, D.C.

Schneider, S. H. 1987. Climate modeling. Scientific American 256:72–80.

Schneider, S. H. 1990. Global warming: are we entering the greenhouse century? Vintage Books, New York. 343 pp.

Schneider, S. H. 1993a. Can paleoclimatic and paleoecological analyses validate future global climate and ecological change projections? Pages 317–340 *in* J. A. Eddy and H. Oeschger, editors. Global changes in the perspective of the past. John Wiley & Sons, Chichester, England.

Schneider, S. H. 1993b. Scenarios of global warming. Pages 9–23 *in* P. Kareiva, J. Kingsolver, and R. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Mass.

Schneider, S. H. 1994. Detecting climatic change signals: are there any "fingerprints"? Science 263:341–347.

Schneider, S. H. 1996. The future of climate: potential for interaction and surprises. Pages 77–113 *in* T. E. Downing, R. S. Chen, R. W. Kates, and M. L. Parry, editors. Climate change and world food security. North Atlantic Treaty Organization ASI Series 137.

Schneider, S.H. 1997. Laboratory Earth: the planetary gamble we can't afford to lose. Basic Books, New York. 174 pp.

Schneider, S. H., and R. Londer. 1984. The coevolution of climate and life. Sierra Club Books, San Francisco. 563 pp.

Schneider, S. H., and S. L. Thompson. 1981. Atmospheric CO_2 and climate: importance of the transient response. Journal of Geophysical Research 86:3135–3147.

Shabalova, M. V., and G. P. Können. 1995. Climate change scenarios: comparisons of paleoreconstructions with recent temperature changes. Climate Change 29:409–428.

Smith, T. M., H. H. Shugart, G. B. Bonan, and J. B. Smith. 1992. Modeling the potential response of vegetation to global climate change. Pages 93–116 *in* F. I. Woodward, editor. Advances in ecological research: the ecological consequences of global climate change. Academic Press, New York.

Stamm, J. F., and A. Gettelman. 1995. Simulation of the effect of doubled atmospheric CO_2 on the climate of north-ern and central California. Climatic Change 30:295–325.

Stouffer, R. J., S. Manabe, and K. Bryan. 1989. Interhemispheric asymmetry in climate response to a gradual increase of atmospheric CO_2. Nature 342:660–662.

Stuart, A. J. 1979. Pleistocene occurrences of the European pond tortoise (*Emys orbicularis* L.) in Britain. Boreas 8:359–371.

Titus, J. G., and V. Narayanan. 1995. The probability of sea-level rise. Climatic Change. U.S. Environmental Protection Agency, Office of Policy, Planning and Evaluation, Climate Change Division, Adaptation Branch, Washington, D.C. 186 pp.

Torn, M. S., and S. J. Fried. 1992. Predicting the impacts of global warming on wildland fire. Climate Change 21:257–274.

Trenberth, K. E., editor. 1992. Climate system modeling. Cambridge University Press, Cambridge, England. 788 pp.

Trenberth, K. E. 1993. Northern Hemisphere climate change: physical processes and observed changes. Pages 35–59 *in* H. A. Mooney, E. R. Fuentes, and B. I. Kronberg, editors. Earth system responses to global change. Academic Press, New York.

Vegetation/Ecosystem Modeling and Analysis Project. 1995. Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochemical Cycles 9:407–437.

Vitousek, P. M. 1993. Global dynamics and ecosystem processes: scaling up or scaling down? Pages 169–177 *in* J. R. Ehleringer and C. B. Field, editors. Scaling physiological processes: leaf to globe. Academic Press, New York.

Washington, W. M., and G. H. Meehl. 1989. Climate sensitivity due to increased CO_2: experiments with a coupled atmosphere and ocean general circulation model. Climate Dynamics 4:1–38.

Washington, W. M., and C. L. Parkinson. 1986. An introduction to three-dimensional climate modeling. Oxford University Press, New York. 422 pp.

Wigley, T. M. L. 1985. Impact of extreme events. Nature 316:106–107.

Wigley, T. M. L., and S. C. B. Raper. 1991. Detection of the enhanced greenhouse effect on climate. Pages 231–242 *in* J. Jager and H. L. Ferguson, editors. Climate change: science, impacts and policy. Cambridge University Press, Cambridge, England.

Wilson, E. O. 1992. The diversity of life. W. W. Norton & Co., New York. 424 pp.

Wright, H. E., J. E. Kutzbach, T. Webb III, W. F. Ruddiman, F. A. Street-Perrott, and P. J. Bartlein, editors. 1993. Global climates since the last glacial maximum. University of Minnesota Press, Minneapolis. 569 pp.

Ye, D. 1989. Sensitivity of climate model to hydrology. Pages 101–108 *in* A. Berger, R. E. Dickinson, and J. W. Kidson, editors. Understanding climate change. American Geophysical Union, Washington, D.C.

Understanding Climate Change Effects on Glacier National Park's Natural Resources

Comanor, P. L., D. B. Fagre, J. D. White, F. R. Hauer, and S. W. Running. 1997. Watershed responses to climate change at Glacier National Park: ecosystem simulation and long-term monitoring. Journal of American Water Resources Association. In press.

Finney, M. A., and K. C. Ryan. 1995. Use of the FARSITE fire growth model for fire prediction in U.S. national parks. Pages 183–189 *in* J. D. Sullivan, J. L. Wybo, and L. Buisson, editors. Proceedings of The International Emergency Management and Engineering Conference, 9–12 May 1995, Nice, France.

Hall, M. H. P. 1994. Predicting the impact of climate change on glacier and vegetation distribution in Glacier National Park to the year 2100. M.S. thesis, State University of New York, Syracuse. 192 pp.

Hungerford, R. D., R. R. Nemani, S. W. Running, and J. C. Coughlan. 1989. MTCLIM: a mountain microclimate simulation model. U.S. Forest Service Research Paper INT–414, Intermountain Station, Ogden, Utah. 52 pp.

Keane, R. E., K. C. Ryan, and S. W. Running. 1996. Simulating the effects of fire on northern Rocky Mountain landscapes using the ecological process model FIRE–BGC. Tree Physiology 16:319–331.

Running, S. W., and S. T. Gower. 1991. FOREST–BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. Tree Physiology 9:147–160.

Running, S. W., R. R. Nemani, D. L. Peterson, L. E. Band, D. F. Potts, L. L. Pierce, and M. A. Spanner. 1989. Mapping regional forest evapotranspiration and photosynthesis by coupling satellite data with ecosystem simulation. Ecology 70:1090–1101.

White, J. D., and S. W. Running. 1994. Testing scale dependent assumptions in regional ecosystem simulations. Journal of Vegetation Science 5:687–702.

White, J., and M. White. 1994. Effects of global climate change on regional snowpack simulation in the Lake McDonald watershed of Glacier National Park. American Water Resources Annual Meeting, 24–26 October 1994, Missoula, Mont. Abstract.