# Climate Change: Overview and Implications for Wildlife

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## Synergisms of Climate Change and Ecology

The Earth's climate is vastly different now from what it was 100 million years ago when dinosaurs roamed the planet and tropical plants thrived closer to the poles. It is different from what it was only 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 natural forces driving the climate—for example, the immense energy input to the Earth from the sun that powers the climate. We can, however, indirectly alter the natural flows of energy enough to create significant climatic 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 that reaches the Earth's surface to warm the climate. Gases in the atmosphere such

as water vapor and $CO_2$, however, trap a large fraction of long-wavelength radiant energy, called terrestrial 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 gases are typically projected to result in a global warming of about 1.5°C to 6°C in the 21st century (IPCC 1990, 1996a, 2001a—the latter reference suggesting the upper range limit of nearly 6°C warming by 2100). This range, especially if beyond 2–3°C (IPCC 2001b), would likely result in ecologically significant changes, which are why climatic considerations are fundamental in the discussion of possible ecological consequences that may involve wildlife.

We may already be feeling the climatic effects of having disturbed 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 and thereby causing deforestation—become large enough, significant global (worldwide) changes are expected. Such modifications 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 (e.g., melted sea ice). We need quantitative evaluations of the potential for human activities to effect physical ecological changes around the globe. Such evaluations are central to potential policy responses to mitigate such global changes (Schneider 1990; IPCC 1996b,c; IPCC 2001b,c).

## Synergisms

The synergistic, or combined, effects of habitat fragmentation and climate change represent one of the most potentially serious global change problems. People destroy or divide natural habitats for farmland, settlements, mines, or other developmental activities. Changes in climate will force individual species of plants and animals to adjust, if they can, as they have in the past. During the Ice Age many species survived by migrating to appropriate habitats. Today such migrations would be much more difficult because they would entail migration across freeways, agricultural zones, industrial parks, military bases,

and cities of the 21st 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.

The Kirtland's warbler in northern Michigan provides one example of syngergism. The 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 tree will move north with warming, but the warbler is not likely to 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 to 60 years. This potential for extinction indicates how the already high rate of extinctions around the world could 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 management problems of anticipating and responding to global change risk. For example, one controversial management plan would be to set up interconnected nature reserves that run north to south or from lower to higher elevation, which could reduce the likelihood of some species being driven to extinction in the event of climate changes. Alternatively, we could simply let the remnants of relatively immobile wildlife and natural plant communities remain in existing isolated reserves and parks, which could lead to some extirpations. 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. To examine such questions in scientific and economic detail, a multidisciplinary examination of various aspects of climatology, economics, and ecology is needed. Here we begin with a background discussion of climatic history, processes, modeling, and validation as a prelude to focusing on ecological processes, which need to be examined in order to project possible synergisms among ecology and climate change.

# Climate History: What Has Happened

Scientists can reconstruct the cyclical expansion and contraction of polar caps and other ice masses from ice core samples taken from Greenland and Antarctica. When snow falls on high, cold glaciers 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. 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. By studying these air bubbles and ice, scientists have been able to determine that 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 to the (current) 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 shifted into their current states (Eddy and Oeschger 1993). These ice cores also provide information on the presence of $CO_2$, an important greenhouse-effect gas. 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 infrared radiative heat trapped in the atmosphere—thus amplifying the cooling—and vice versa 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 industrial age during the last few centuries.

The transition from extensive glaciation of the Ice Age to the more hospitable landscapes of the Holocene took from 5000 to 10,000 years, during which time the average global temperature increased 5–7°C and the sea level rose some 100 meters. Thus we estimate that natural rates of warming on a sustained global basis are about 0.5°C to 1°C per thousand years. In addition to the sustained rates, there is growing evidence of rapid so-called abrupt nonlinear changes as well (Severinghaus and Brook 1999). Both the slower and more rapid changes were large enough to have radically

influenced where species live and to have potentially contributed to the well-known extinctions of large animals (e.g., woolly mammoths, sabertooth cats, and enormous salamanders).

A large interdisciplinary team of scientists, including ecologists, palynologists (scientists who study pollen), paleontologists (scientists who study prehistoric life, especially fossils), climatologists, and geologists, formed a research consortium (Cooperative Holocene Mapping Project 1988, Wright et al. 1993) to study the dramatic ecological changes accompanying the transition from Ice Age to the recent interglacial period. 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, coniferous tree pollen, now the dominant pollen type in the boreal zone 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, investigated multiple pollen types, including not only boreal species but also herbs and more arid (xeric) species, as well as oaks and other mesic species.

They discovered 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 and combinations of pollen types provided no analogous associations to today's vegetation communities (Overpeck et al. 1992). That is, whereas all species moved, they moved at different rates and directions, not as groups. Consequently, the groupings of species during the transition period were often dissimilar to those present today. The relevance of this is that, in the future, ecosystems will not necessarily move as a unit as climate changes (even if there were time and space enough for such a migration).

Past vegetation responses to climate change at a sustained average rate of 1°C per millennium indicates that credible predictions of future vegetation changes cannot neglect transient (i.e., time-evolving) dynamics of the ecological system. Furthermore, because the forecasted global average rate of temperature increase over the next century or two exceeds those typical of the sustained average rates experienced during the last 120,000 years, it is unlikely that paleoclimatic conditions reconstructed from millennial time scale conditions would be near analogs for a rapidly changing anthropogenically warmed world (e.g., see Schneider and Root 1998, from which some of this chapter is adapted). Future climates may not only be quite different from more recent past climates, they may also be quite different from those inferred from paleoclimatic data and from those to which some existing species are evolutionarily adapted. Therefore, past changes do provide a backdrop or context to gauge future changes, but not primarily as a spatial analog; rather as means to verify the behavior of models of climate or ecosystem dynamics that are then used to project the future conditions given the rapid time-evolving patterns of anthropogenic forcing (Crowley 1993, Schneider 1993a).

## Forces of Climate Change

Causes of climate change are broadly categorized as external and internal. These terms, however, are defined relative to the focus of study; 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. External

causes of climate change do not have to be physically external to the Earth (such as the sun), but do occur outside of the climate system under examination. If our focus is on atmospheric change on a one-week time scale (i.e., the weather), the oceans, land surfaces, biota, and human activities that produce $CO_2$ are all external (i.e., 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 all 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.

Fluctuations in heat radiated by the sun—perhaps related to varying sunspots—are external to the climate system. Influences of the gravitational tugs of other planets on the Earth's orbit are also external. Human-caused changes in the Earth's climate could not perceptibly alter either one of these cycles. Carbon dioxide and methane levels rise and fall with ice age cycles, meaning they are certainly internal on a 10,000-year time scale. But on a 20-year scale these greenhouse gases become largely an external cause of climate change because small changes in climate have little feedback effect on, for example, humans burning fossil fuels or clearing land.

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

Snow and ice are important factors in climate change because they have higher albedo 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 both sea ice and 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. When the atmosphere rubs on the ocean, the ocean responds by modifying 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).

## Climate Change Projections: What May Happen?

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. 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 activities affecting pollution or land use over the next century. The next step is to estimate the response of the various components of the Earth system to such 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 allows a modeling 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 (e.g., Schneider 2001). Because models are not perfect replicas of the actual natural system, they must be tested against the expanding base of field and laboratory data. This not only allows assessment of the credibility of current simulations, 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 21st century projections both for human population size and affluence show drastic increases when aggregated over less highly developed countries and more highly developed countries. 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), carbon emissions are typically predicted to rise several-fold over the next 100 years. Making such projections credibly is difficult. Therefore analysts disagree by as much as a factor of 10 about how much $CO_2$ will be emitted by 2100 (Johansson et al. 1993, IPCC 1996c, Nakicenovic and Swart 2000). Specific scenarios are debatable because the amount of carbon emitted through human activities will significantly depend on social-structural projections, such as what kinds of energy systems will be developed and deployed globally and what the standards of living will be over the next several decades, not to mention population growth.

To turn estimates of $CO_2$ emissions into estimates of $CO_2$ concentrations in the atmosphere, which is 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 was estimated during the last few decades of the 20th century at about 50%, because the amount of $CO_2$ buildup in the atmosphere each year (about 3 billion tons of carbon as $CO_2$) was 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, and oceanic and atmospheric subcomponents (IPCC 1996a,b and 2001a). The estimated $CO_2$ concentration can then be fed into computerized climatic models to estimate its effects on climate (e.g., Wigley and Schimel 2000).

Climate prediction, like most other forecasts involving complex systems, generally involves subjective judgments (e.g., see Moss and Schneider 2000). 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 in 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 called 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 (GCMs), 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).

## *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 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 5–7°C glacial/interglacial cycle). General circulation models map the seasonal cycle well. This supports the scientific consensus about the plausibility of global warming of several degrees in the 21st 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 significant effects on the decade- to century-long time scales over which atmospheric $CO_2$ is expected to double.

A second verification technique involves isolating individual physical components of the model and testing them against actual data. A model should reproduce the flow of thermal energy among the atmosphere, the surface, and space with no more than about a 10 to 20% 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.

A third validation method involves a 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 paleorecords that serve as a proxy for climatic conditions of the ancient Earth. This method may even include testing the model's 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.

Using these techniques, much has been learned from examining the global climatic trends of the past century. The years 1997 and 1998 were the warmest years on record for the Earth's surface in the

past century; at the same time the stratosphere was at its coldest (IPCC 1996a and 2001a). 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 30% increase in $CO_2$, a 150% increase in $CH_4$, and the introduction of human-generated heat-trapping chemicals such as chlorofluorocarbons and halons. Industrial activities since the 1950s have contributed to the increase of sulfur dioxide and other aerosol particles into the atmosphere, the net effect of which is likely to reduce surface temperature by reflecting sunlight back to space. This is complicated by the fact that light hazes like sulfur oxides reflect much more radiation than they absorb but dark particles like soot produced in fires or diesel engines can warm the climate by absorbing more energy than they reflect. The IPCC (2001a) estimates the net effect to be a cooling, with a large range of uncertainty. Although such cooling effects may have counteracted global warming by only several tenths of a degree, the hazes occur regionally and could be producing ecologically significant, unexpected regional changes in climate patterns (Schneider 1994).

Although the 0.6°C ± 0.2°C surface warming in the 20th century is consistent with the human-induced greenhouse gas buildup, some have argued that this warming could possibly be largely natural—either a natural internal fluctuation of the system or driven by natural forcing like a change in the energy output of the sun. However, the IPCC (2001a) assessment states on page 11 of the Summary for Policymakers that there is too much consistent evidence of a human influence to assign all the 20th century warming to natural causes: "There is new and stronger evidence that most of the warming observed over the last 50 years is attributable to human activities" (for estimates of the subjective probability of human induced global warming amounts given a doubling of $CO_2$, see Morgan and Keith, 1995). However, if one argues that there could have been a natural warming trend in the 20th century, then by symmetry it is also not possible to rule out the converse that, independent of the enhanced greenhouse effect due to human activity, there was a natural cooling fluctuation taking place during the 20th century. If so, the world would then have warmed up much more than observed had we not had such a fortuitous natural cooling trend. One could even speculate that the dramatic temperature rise since the 1970s with global high temperature records reflects the termination of a

natural cooling trend combined with the rapid establishment of the expected enhanced greenhouse effect. We are certainly not suggesting this to be the most probable case, simply showing why a fairly wide range of possibilities is plausible given the remaining uncertainties.

Santer et al. (1996) suggest that when aerosols and greenhouse gas forcings are combined, climate models more closely match 30 years of observations. Nevertheless, wide ranges of climate sensitivities—from as low as a 0.5°C warming to well above a 5.0°C warming (e.g., Wigley and Raper 2001, Andronova and Schlesinger 2000)—are still consistent with current observations. 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 (e.g., 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. As mentioned previously, though, the ecologically important forecasts of time-evolving regional climatic changes are much less credible than global-average projections and require that ecologists use many alternative scenarios of possible climatic changes. IPCC (2001a) suggests that by the end of the 21st century, there will likely be overall warming between about 1.5 and 6°C; land will warm more than oceans, and higher latitudes more than tropical latitudes; precipitation will increase on average; midlatitude, midcontinental drying in summer is likely in some areas, and the hydrological cycle will intensify thus raising the possibility of enhanced extremes like droughts and floods, as well as more extreme heat waves and fewer cold snaps. Increased intensity of tropical cyclones is considered likely, but frequency changes remain speculative. In short, the future climate could be very altered from that to which modern ecosystems have become adapted.

In summary, no clear physical objection or direct empirical evidence has contradicted the consensus of scientists (IPCC 1990, 1996a, 2001a; NAS 2001) that the world is warming, nor has credible evidence emerged to contradict the substantial probability that temperatures will rise because of increases in greenhouse gases (Morgan and Keith 1995). Even in the mid-1990s many scientists thought the evidence sufficient to believe that recently observed climatic variations and human activities are probably connected (Karl

et al. 1995). The IPCC (1996a, page 5) carefully weighed the uncertainties and concluded that "[n]evertheless, the balance of evidence suggests that there is a discernable human influence on global climate." The IPCC (2001a) reinforces and strengthens that judgment, particularly since recent studies of the past 1000 years (Mann et al. 1999) show that for the Northern Hemisphere the last half of the 20th century is likely to be warmer than at any time during the past 1000 years.

## Relevance of Climate Modeling to Regional Climate Change and Ecosystem Studies

Scientists who estimate the future climatic changes that are relevant to ecosystems have focused on the GCMs 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 GCMs and the capabilities of even the most advanced computers (IPCC 1990, 1996a, 2001a). Simulating 1 year of weather in 30-minute time steps with the crude resolution of 40 latitudinal lines × 48 longitudinal lines and 10 vertical layers—nearly 20,000 grid cells around the globe—takes many minutes on a supercomputer. This level of resolution, however, cannot resolve the Sierra Nevada of California and the Rocky Mountains as separate mountain chains. Refining the resolution to 50-square-kilometer grid squares or less would so dramatically increase the number of computations that it could take roughly months of computer time to simulate weather statistics for one year.

Even the highest-resolution, three-dimensional GCMs will not have a grid with nodes much less than 10 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, GCMs 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. It is, nonetheless, important to have climatic forecasts and ecological-

response analyses on the same physical scales (Root and Schneider 1993).

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, because 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 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.

## *Regional Changes*

Although the consensus among researchers about the plausibility of significant human-induced global climate change is growing, no assessment (e.g., IPCC 1996c, 2001a) has suggested the existence of a strong consensus about how that global climate 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 that has been 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 confidently.

Even more uncertain than regional averages, but perhaps more important to long-term ecosystem responses (Parmesan et al. 2000), are estimates of climatic variability during the transition to a new equilibrium, particularly at the regional scale. These 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, 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, Knutson 1998). Such changes would significantly affect susceptible terrestrial and marine ecosystems (Doyle 1981, O'Brien et al. 1992).

## *Downscaling Climate Predictions to Regional Effects*

### 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. As mentioned above, 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 (GCM). 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.

A 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 (e.g., state-sized) scales. This map shows 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 provided. 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 map 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 (greenhouse) 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 climate 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 21st century (Schneider 1993b).

Therefore, techniques to shrink climate forecasts that use current distributions of environmental variables at local scales and cor-

relate them with current large-scale regional patterns will not necessarily provide a good guideline about how large-scale patterns would be distributed regionally. 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.

### Regional-Scale Models with GCM Inputs

Other techniques can still translate large-scale patterns to smaller scales, but these techniques are based on known processes rather than on empirical maps of 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 GCM. In essence, this approach uses a mesoscale model (i.e., 10–50-kilometer grid cells) based on physical laws to solve the problem of translating GCM 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 downscaling techniques. Neither are the problems of GCMs entirely eliminated by mesoscale grids, because such grids are bigger than individual clouds or trees. But such methods do bring climate-model scales and ecological-response scales much closer.

## 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 plant species with physical factors such as temperature, soil moisture, 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. 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); the 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, but they have some serious drawbacks as well. That is, they are typically static, not time-evolving dynamic simulations, and thus cannot capture the transient sequence of changes that would take place in reality. In addition, such static biome models occasionally make "commission errors"—they predict vegetation types to occur in certain zones where climate would indeed permit such vegetation, but other factors like soils, topography, or disturbances like fire actually preclude it. Furthermore, local patterns may influence vegetation dynamics at scales not captured in some simulations, and seed germination and dispersal mechanisms are also either not explicitly simulated or simulated only crudely with such models. Remarkably they are still able to produce generalized maps of vegetation types that do indeed resemble current or even paleoclimatic patterns in a broad sense. Their details, however, do not provide confident projections for future vegetation states. Fortunately, progress is being made to include some of the deficiencies mentioned above, and so-called dynamical global vegetation models are being developed to treat the transient nature of vegetation change that would likely accompany climate change.

## *Predicting Animal Responses to Climate Change*

Scientists of the U.S. Geological Survey (USGS), 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 USGS, shifts in bird ranges and densities can be examined. Because these censuses were begun in the 1960s, 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, 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. Then, by using a GCM to forecast how doubling of $CO_2$ would affect the climate variables in the models, he applied statistical models to predict the possible shape and location of the birds' ranges.

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 new areas, provided habitat is available and no major barriers exist. Such shifting of ranges and abundances could cause local extirpations 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, such detailed maps should be viewed only as illustrative of the potential for very significant shifts with 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 herpetofauna (or herps), are different from birds in many ways that are important to our discussion. First, because herps 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 to allow them to respire through their skin. Third, herps are not able to disperse as easily as birds, and the habitat

through which they crawl must not be too dry or otherwise impassible (for example, high mountains or busy 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 (Parmesan et al. 2000). Rapid movements by birds are possible because they can fly, but for herps such movements are much more difficult. For example, R. L. Burke (then at University of Michigan, Ann Arbor, pers. comm. 1995) 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 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 herp 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. L. Root (pers. comm. 1995) performed a preliminary analysis of North American herp ranges in an attempt to determine which, if any, are associated with climatic factors such as temperature, vegetation-greening duration, and solar radiation. Their evidence suggests that northern boundaries of some species ranges are associated with these factors, implying that climate change could have a dramatic impact on the occurrence of these species (e.g., see Schneider and Root 1998 for details and a literature survey). Furthermore, most North American turtles and several other reptile species could exhibit vulnerability to climate change because the temperature experienced as they develop inside the egg determines their sex. Such temperature-dependent sex determination makes these animals uniquely sensitive to temperature change, meaning that climate change could potentially cause severely skewed sex ratios, which could result in dramatic range contractions. Many more extinctions are possible in herps than in birds because the forecasted human-induced climatic changes could occur rapidly when compared with the rate of natural climatic changes, and because the dispersal ability of most herps is painfully slow, even without considering the additional difficulties associated with human land-use changes disturbing their migration paths.

In general, animals most likely to be affected earliest by climate

change are those in which populations are fairly small and limited to isolated habitat islands. 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). Recent studies of small mammals in Yellowstone National Park show that statistically significant changes in both abundances and physical sizes of some species 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 1997). Therefore, climate change in the 21st century could likely cause substantial alteration to biotic communities, even in protected habitats such as Yellowstone National Park.

## Current Animal Responses to Climate Change

Animals are showing many different types of changes related to climate. These include changes in ranges; abundances; phenology (timing of an event); morphology and physiology; and community composition, biotic interactions, and behavior. Changes are being seen in all different types of taxa, from insects to mammals, and on many of the continents (Price et al. 2000). For example, the ranges of butterflies in Europe and North America have been found to shift poleward and upward in elevation as temperatures have increased (Pollard 1979, Parmesan 1996, Ellis et al. 1997, Parmesan et al. 1999). From 1979 to 1989, population densities of the Puerto Rican coqui (*Eleutherodactylus coqui*) showed a negative correlation with the longest dry period during the previous year (Stewart 1995). Similarly, the disappearance of the golden toad (*Bufo periglenes*) and the harlequin frog (*Atelopus varius*) from Costa Rica's Monteverde Cloud Forest Reserve seemed to be linked to the extremely dry weather associated with the 1986–87 El Niño–Southern Oscillation (Pounds and Crump 1994). Birds' ranges reportedly have extended poleward in Antarctica (Fraser et al. 1992, Emslie et al. 1998), and Europe (Thomas and Lennon 1999). For instance, the northern movement of the spring range of barnacle geese (*Branta leucopsis*) along the Norwegian coast correlates significantly with an increase in the number of April and May days with temperatures above 6°C (Prop et al. 1998). Reproductive

success of the California quail (*Calipepla californica*) is positively correlated with the previous winter's precipitation (Botsford et al. 1988). Rainfall affects the chemistry of plants eaten by quail, with the plants producing phytoestrogens, compounds similar to hormones that regulate reproduction in birds and mammals. Drought-stunted plants tend to have higher concentrations of these compounds (Leopold et al. 1976). The northern extension of the porcupine's (*Erethizon dorsatum*) range in central Canada has been associated with a warming-associated poleward shift in the location of tree line (Payette 1987). In the United Kingdom, the dormouse (*Muscardinus avellanarius*) has disappeared from approximately half of its range over the last 100 years (Bright and Morris 1996). This disappearance appears to be linked to a complex set of factors including climatic changes, fragmentation, and the deterioration and loss of specialized habitat.

Warmer conditions during autumn–spring adversely affect the phenology of some cold-hardy insects. Experimental work on spittlebugs (*Philaenus spumarius*) found that they hatched earlier in winter-warmed (3°C above ambient) grassland plots (Masters et al. 1998). Chorusing behavior in frogs, an indication of breeding activities, appears to be triggered by rain and temperature (Busby and Brecheisen 1997). Two frog species, at their northern range limit in the United Kingdom, spawned 2 to 3 weeks earlier in 1994 than in 1978 (Beebee 1995). Three newt species also showed highly significant trends toward earlier breeding, with the first individuals arriving 5 to 7 weeks earlier over the course of the same study period. This study also examined temperature data, finding strong correlations with average minimum temperature in March and April (negative) and maximum temperature in March (positive) for the two frogs with significant trends, and a strong negative correlation between lateness of pond arrival and average maximum temperature in the month before arrival for the newts. Using less precise methods, a family of naturalists in England recorded the timing of first frog and toad croaks for the period from 1736 to 1947 (Sparks and Carey 1995). The date of spring calling for these amphibians became earlier over time, and was positively correlated with spring temperature, which was positively correlated with year. Changes in phenology or links between phenology and climate have been noted for earlier breeding of some birds in the United Kingdom (Thompson et al. 1986), Germany (Winkel and Hudde 1996, Ludwichowski

1997) and the United States (Brown et al. 1999). Changes in bird migration have also been noted with earlier arrival dates of spring migrants in the United States (Ball 1983), later autumn departure dates in Europe (Bezzel and Jetz 1995), and changes in migratory patterns in Africa (Gatter 1992).

The effect of temperature on the metabolism of dormant horned toads in Brazil was found to be stronger than the effect on resting toads at most temperatures (Bastos and Abe 1998). Reptile physiology is temperature sensitive also. Painted turtles grew larger in warmer years, and during warm sets of years turtles reached sexual maturity faster (Frazer et al. 1993). Physiological effects of temperature can also occur while reptiles are still within their eggs. Leopard geckos (*Eublepharis macularius*) produced from eggs incubated at a high temperature of 32°C showed reproductive behavioral changes and possible female sterility (Gutzke and Crews 1988). Spring and summer temperatures have been linked to variations in the size of the eggs of the pied flycatcher (*Ficedula hypoleuca*) (Järvinen 1996). The early summer mean temperatures explaining approximately 34% of the annual variation in egg size between the years 1975 and 1994. Body mass, which correlates with many life-history traits including reproduction, diet, and size of home ranges of the North American wood rat (*Neotoma* spp.) has shown a significant decline inversely correlated with a significant increase in temperature over the last 8 years in one arid region of North America (Smith et al. 1998). In studies of spring temperature effects on red deer (*Cervus elaphus*) in Scotland, juvenile deer grew faster in warm springs leading to increases in adult body size, a trait positively correlated with adult reproductive success. In Norway, red deer born following warm winters (that have more snow) were smaller than those born after cold winters—a difference persisting into adulthood (Post et al. 1997).

Differential responses by species could cause existing animal communities to undergo a reformulation (Root and Schneider 1993). Peach–potato aphids grown on plants kept in elevated $CO_2$ (700 ppm) showed a reduced response to alarm pheromones in comparison to those grown on plants in ambient $CO_2$ (350 ppm) (Awmack et al. 1997a). The aphids were more likely to remain on leaves, rather than move away, in response to the pheromones, possibly making them more susceptible to predators and parasitoids. Temperature and dissolved-oxygen concentrations can alter the

behavior of amphibian larvae, and changes in thermal environments can alter the outcome of predator–prey interactions (Moore and Townsend 1998). Climate change may be causing mismatching in the timing of breeding of great tits (*Parus major*) in the United Kingdom and other species in their communities (Visser et al. 1998). Post et al. (1999) documented a positive correlation between gray wolf (*Canis lupus*) pack size in winter and snow depth on Isle Royale (U.S.). In years with deeper snow, wolves formed larger packs, which led to more than three times as many moose kills.

## *Top-Down Approaches*

The biogeographic approach just summarized is an example of a top-down technique (like that of the Holdridge life-zone classification), in which data on abundances or range limits of species, 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 driven by given climate changes.

## *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 (Idso and Kimball 1993) or even a single leaf to understand how, for example, increased atmospheric $CO_2$ concentrations might directly enhance photosynthesis, net primary production, or water-use efficiency. Most studies such as these indicate increases in all these factors, increases that some researchers have extrapolated to ecosystems (Idso and Brazel 1984, Ellsaesser 1990).

However, 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 turn, would increase transpiration, thereby offsetting 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 negative feedback effect (or "emergent property" of the coupled forest atmosphere system) 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 to produce highly confident conclusions without some sort of validation testing at the scale of the system under study.

## *Combined Top-Down and Bottom-Up Approaches*

To help resolve the deficiencies of the top-down 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 climate change scenarios. 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. Growing degree-days (related to average temperature but not average temperature per se) are used in this scenario.

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 ranges (Pacala and Hurtt 1993). (The fundamental range is the geographic space in which a given species could theoretically survive—for example, if its competitors were absent—and the realized range is where it actually exists.) The question then is, What

limits the realized range, 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. 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 Järvis (1993:121) states, "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 (SCS). 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 climate 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. According to Levin (1993:14), "Although it is well understood that correlations are no substitute for mechanistic understanding of relationships, correlations can play an invaluable role in suggesting candidate mechanisms for (small-scale) investigation." SCS, 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 assess-

ment process (see also Vitousek 1993, Harte and Shaw 1995), which is why *strategic* is the first word in SCS.

## *Bird Case Study*

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, IPCC 2001a). 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. The National Audubon Society has volunteer forces amassed to aid in the collection of Christmas Bird Count data. By using these data, Root determined that for a large proportion of species, average distribution and abundance patterns are associated with various environmental factors (e.g., northern range limits of some species are apparently limited by average minimum January temperature [Root 1988a,b,c, 1989; Repasky 1991]).

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 1988b). 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. Preliminary results indicate that temperatures are more likely than day length to explain this effect (Root 2000). 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 (Root

1994). No claim is made at this point in the research for the generality of the preliminary results indicating strong and quantitative links between bird distributions and climate change. This example does permit, however, a clear demonstration of refined methods for cycling across scales to estimate ecological responses to climate change.

## Three-Way Linkages and Community Ecology

The anticipated changes in plant ranges will probably have dramatic effects on animals, both on the large biogeographic scale and on the local 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). 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 these animals. If the climate changes more rapidly than the dispersal rates of the plants, it could 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 become extinct.

Many animal species have ranges that are not directly limited by vegetation but are instead restricted by temperature (Root 1988c). 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). 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 (Root and Schneider 1993). 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 climate change on animals, the three-way linkages among animals, plants, and climate need to be investigated. Animals and plants affect each other and are affected by climate. At the same time, altered surface vegetation can affect climate because mid-continental summer precipitation is significantly influenced by water vapor from evapotranspiration (Ye 1989, Salati and Nobre 1991).

## A Discernible Impact of Climate on Wildlife in the 20th Century?

Attributing observed changes in populations of plants and animals to climate change, specifically temperature increases, is possible because the patterns created by this large-scale pressure (global warming) are broad, often predictable, and generally continuous, rather than spotty. Additionally, these changes are expected to be concentrated in areas where the temperature change is largest, and less evident elsewhere. Certainly, climate change is only one of a long list of pressures influencing population distributions, health, morphology, and traits such as timing of activities. Other key pressures include: conversion of natural and semi-natural habitats, human persecution (e.g., legal and illegal by-catch, harassment), wildlife trade, war and other civil conflict, pollution and other biochemical poisoning, introduction of exotic species, and physical obstructions (e.g., roads, farm fields, tall towers, and buildings). Changes caused by these localized pressures would create a pattern of response that is irregular and patchy, and often centered around rapidly developing areas. Therefore, to document a strong role for climate in explaining many of the observed changes in animal and plant populations, increased confidence is obtained using examples that, when observed over a decade or longer and over large spatial scales, show changes in the direction predicted by the physiological tolerances of the particular species. The result—a "fingerprint"—of a coherent large-scale pattern exhibited in many species around the globe, which is consistent with the understanding of the causal

mechanisms, provides the greatest confidence in the attribution of observed changes in wildlife or plants to global climate change.

Using information from the literature, Root et al. (2001) examined if animals and plants are already exhibiting a discernible change consistent with changing temperatures and predicted by our understanding of the physiological constraints of species. They amassed over 1300 research papers with keywords concerning climate and animals and used the literature assessed by Chapter 5 of IPCC (2001b) for plants (over 1000 articles). Of these, over 500 address changes over time, with around 100 studies analyzing at least 10 years of data. A priori, they developed three criteria to determine which of these studies would be included in their analysis. Each article met at least two of the following three criteria: (1) a trait of at least one animal or plant must show a statistically significant positive or negative change over time, (2) changes in this trait need to correlate significantly with changes in local temperature, and (3) local temperature must significantly change with time. The 45 studies meeting these criteria report significant and nonsignificant findings on more than 450 animal species in Europe, North America, Central America, the Southern Ocean islands, Antarctica, along the North American shoreline of the Pacific Ocean, in the North Pacific Ocean, and in the Antarctic Ocean, and approximately 50 plant species (in Europe, North America, and Antarctica). Of these 500 species, around 440 (88%) exhibit a significant change over time, and 84% (about 370) of these 440 species exhibit change in a manner predicted, based on the physiology of the species (an application of the SCS technique of Root and Schneider 1995).

## Documented Responses of Animals and Plants Used in IPCC Third Assessment Report

Forty-five studies were included in these analyses for the IPCC Third Assessment Report (TAR). The number would be higher if Root et al. (2001) had examined other climatic variables in addition to temperature, which is the variable predicted with most confidence to change with increasing greenhouse gases (IPCC 1996a). Precipitation (e.g., drought) was not considered in the IPCC effort primarily for three reasons: (1) It is more difficult to use than temperature to determine mechanisms of how changing precipitation

might influence many animals. (2) It is more difficult to use than temperature to determine how precipitation changed in the past at local scales because of its high degree of regional heterogeneity. (3) How precipitation may change in the future is more difficult to model confidently than temperature. Additionally, the effects of temperature on the physiology of species are fairly well understood and reliably demonstrated in the literature to cause changes in traits of species (Root 1988c). These 45 studies indicate significant changes are occurring in Europe and northern Africa (32 studies), North America (6 studies), Central America (1 study), Antarctica (2 studies), Southern Oceanic islands (1 study), the North American Pacific Ocean shoreline (1 study), the North Pacific Ocean (1 study), and the Antarctic Ocean (1 study) (Table OV.1). If drought had been included, then studies from many other regions, such as Australia and Asia, would have been included. Of those species exhibiting change (about 90%), the vast majority (about 80%) show changes consistent with a hypothesized response to climate warming.

Quantifying such a wide array of changes is problematic. Meta-analyses, however, provide a statistical method of summarizing results from many studies, even though such studies may not use common methods or databases (Hedges and Olkin 1985). If warming causes changes in phenology, then it would be reasonable to expect that phenological changes observed regionally might be associated with regional temperature changes. To test this hypothesis, Root et al. (2001) performed a meta-analysis on all 18 animal studies (195 species), and a meta-analysis on 4 plant studies (49 species) reporting spring phenological changes (Table OV.2).

Eight animal studies lacked information needed to determine correlation coefficients ($r$). Consequently, Root et al. (2001) performed two types of meta-analyses on these data: one taking advantage of the $r$ values that were reported (12 studies, 34 species),[1] and a second including all 18 studies and 193 species, but only taking into account the sign of the phenological change (i.e., negative for earlier in the year and positive for later). A meta-analysis using 49 plant species was also performed. The meta-analysis of the correlation coefficients between animal traits and time of year allows one to make an estimate of a common fingerprint—a common correlation coefficient underlying the several studies (see Hedges and Olkin [1985] for more detail on the method). The estimated under-

## Table OV.1. Information from 45 Studies Used by the IPCC (2001b).

| Location | Taxa | Number of Species Exp | No Chg | Opp | Type of Change | Citation |
|---|---|---|---|---|---|---|
| Antarctic Ocean | Invertebrates | 2 | 0 | 0 | Density | Loeb et al. 1997 |
| Antarctica | Birds | 2 | 0 | 0 | Shift Range and Density | Fraser et al. 1992, Smith et al. 1999 |
| Antarctica | Vascular Plants | 2 | 0 | 0 | Density | Smith 1994 |
| Central America | Amphibians | 20 | 30 | 0 | Shift Range and Density | Pounds et al. 1999 |
| Central America | Reptiles | 2 | 1 | 0 | Shift Range and Density | Pounds et al. 1999 |
| Central America | Birds | 15 | 0 | 0 | Shift Range and Density | Pounds et al. 1999 |
| Europe | Invertebrates | 5 | 0 | 0 | Spring Phenology | Fleming and Tatchell 1995 |
| Europe | Invertebrates | 4 | 0 | 0 | Spring Phenology | Zhou et al. 1995 |
| Europe | Invertebrate | 1 | 0 | 0 | Spring Phenology | Visser et al. 1998 |
| Europe and Northern Africa | Invertebrates | 34+ | 17+ | 1+ | Shift Range and Density | Parmesan et al. 1999 |
| Europe | Invertebrates | 1 | 0 | 0 | Morphology | De Jong and Brakefield 1998 |
| Europe | Invertebrate | 1 | 0 | 0 | Genetics | Rodriguez-Trelles et al. 1998 |
| Europe | Amphibian | 1 | 0 | 0 | Spring Phenology | Forchhammer et al. 1998 |
| Europe | Amphibians | 5 | 0 | 0 | Spring Phenology | Beebee 1995 |
| Europe | Amphibian | 1 | 0 | 0 | Morphology | Reading 1998, Reading and Clarke 1995 |

Table OV.I. *Continued*

| Location | Taxa | Number of Species | | | Type of Change | Citation |
|---|---|---|---|---|---|---|
| | | Species | No | Opp | | |
| Europe | Bird | 1 | 0 | 0 | Morphology and Spring Phenology | Järvinen 1989, 1994 |
| Europe | Birds | 0 | 0 | 1 | Spring Phenology | Forchhammer et al. 1998 |
| Europe | Birds | 51 | 0 | 14 | Spring Phenology | Crick et al. 1997, Crick and Sparks 1999 |
| Europe | Bird | 1 | 0 | 0 | Spring Phenology | Ludwichowski 1997 |
| Europe | Bird | 1 | 0 | 0 | Spring Phenology | McCleery and Perrins 1998 |
| Europe | Bird | 1 | 0 | 0 | Spring Phenology | Slater 1999 |
| Europe | Bird | 1 | 0 | 0 | Spring Phenology | Winkel and Hudde 1996 |
| Europe | Bird | 1 | 0 | 0 | Spring Phenology | Visser et al. 1998 |
| Europe | Birds | 3 | 0 | 0 | Spring Phenology | Winkel and Hudde 1997 |
| Europe | Birds | 122 | 0 | 24 | Spring Phenology | Sparks 1999, Mason 1995 |
| Europe | Bird | 1 | 0 | 0 | Fall Phenology | Bezzel and Jetz 1995 |
| Europe | Birds | 27 | 6 | 13 | Fall Phenology | Gatter 1992 |
| Europe | Bird | 1 | 0 | 0 | Shift Range and Density | Bergmann 1999 |
| Europe | Bird | 1 | 0 | 0 | Shift Range and Density | Prop et al. 1998 |
| Europe | Birds | 56 | 7 | 38 | Shift Range and Density | Thomas and Lennon 1999 |
| Europe | Birds | 0 | 0 | 2 | Density | Forchhammer et al. 1998 |

| Europe | Mammals | 7 | 0 | 0 | Morphology | Post and Stenseth 1999 |
|---|---|---|---|---|---|---|
| Europe | Forbs | 11 | 0 | 1 | Spring Phenology | Post and Stenseth 1999 |
| Europe | Tree | 1 | 0 | 0 | Spring Phenology | Walkovszky 1998 |
| Europe | Trees and Shrubs | ? | ? | ? | Spring and Fall Phenology | Menzel and Fabian 1999 |
| Europe | Mt. Plants | ? | ? | ? | Shift Range | Grabherr et al. 1994, Pauli et al. 1996 |
| Europe | Tree | 1 | 0 | 0 | Morphology | Hasenauer et al. 1999 |
| North America | Bird | 1 | 0 | 0 | Spring Phenology | Brown et al. 1999 |
| North America | Bird | 1 | 0 | 0 | Spring Phenology | Dunn and Winkler 1999 |
| North America | Birds | 15 | 0 | 4 | Spring Phenology | Bradley et al. 1999 |
| North America | Mammals | 3 | 0 | 0 | Morphology | Post and Stenseth 1999 |
| North America | Grasses | 6 | 0 | 0 | Density | Alward et al. 1999 |
| North America | Forbs | 24 | 0 | 11 | Spring Phenology | Bradley et al. 1999 |
| North America | Tree | 1 | 0 | 0 | Morphology | Barber et al. 2000 |
| North American | Tree | 1 | 0 | 0 | Spring Phenology | Bradley et al. 1999 |
| S. Ocean Islands | Bird | 1 | 0 | 0 | Shift Range and Density | Cunningham and Moors 1994 |
| N. Am. Shoreline | Invertebrates | 15 | ? | 3 | Density | Sagarin et al. 1999 |
| N. Pacific Ocean | Fish | 1 | 0 | 0 | Morphology | Ishida et al. 1995 |

Includes location of the study, taxa of the species examined, number of species changing, either significantly or non-significantly, in the direction expected with temperature change based on physiological studies (Exp), the number exhibiting no change (No chg), the number significantly or non-significantly changing opposite to that expected (Opp), the type of change observed, and the citation. When the number of species is not specified in the citation, then "?" is used. (After Root et al., 2001.)

lying common correlation is -0.38, which is statistically significantly different from zero ($P < 0.05$) with a 95% confidence interval of $-0.45 \leq r \leq -0.31$. Consequently, a strong pattern of consistent change—a shift toward earlier spring activities—is occurring among those species with negative changes in some measure of their spring phenology.

The "vote counting" meta-analysis of all animals included in spring phenology studies incorporated data for species for which either a correlation coefficient or slope of the relationship between the changing species trait and time was reported. In total, Root et al. (2001) analyzed data with this method for 195 species from 17 studies (Table OV.2). This vote-counting statistic is based on the

Table OV.2. Information from 21 Studies Addressing Changes in Spring Phenology Used by the IPCC (2001b).

| Taxa | Species | No. of Years | Corr Coef | P | Sign | Type of Change | Citation |
|---|---|---|---|---|---|---|---|
| Invertebrate | Drepanosiphum platanoidis | 25+ | ? | 0.0001 | — | Peak Abundance | Fleming and Tatchell 1995 |
| Invertebrate | Elatobium abietinum | 25+ | ? | 0.0001 | — | Peak Abundance | Fleming and Tatchell 1995 |
| Invertebrate | Microlophium carnosum | 25+ | ? | 0.0001 | — | Peak Abundance | Fleming and Tatchell 1995 |
| Invertebrate | Periphyllus testudinaceus | 25+ | ? | 0.0001 | — | Peak Abundance | Fleming and Tatchell 1995 |
| Invertebrate | Phorodon humuli | 25+ | ? | 0.0001 | — | Peak Abundance | Fleming and Tatchell 1995 |
| Invertebrate | caterpillar | 23 | ? | ‹0.05 | — | Peak Abundance | Visser et al. 1998 |
| Invertebrate | Brachycaudus helichrysi | 28 | ? | ‹0.05 | — | Peak Abundance | Zhou et al. 1995 |
| Invertebrate | Sitobion avenae | 28 | ? | ‹0.05 | — | Peak Abundance | Zhou et al. 1995 |
| Invertebrate | Metopolophium dirhodum | 28 | ? | ‹0.05 | — | Peak Abundance | Zhou et al. 1995 |
| Invertebrate | Myzus persicae | 28 | ? | ‹0.05 | — | Peak Abundance | Zhou et al. 1995 |
| Amphibian | Triturus vulgaris | 17 | -0.78 | ‹0.001 | — | Breeding | Beebee 1995 |
| Amphibian | T. cristatus | 17 | -0.59 | ‹0.02 | — | Breeding | Beebee 1995 |
| Amphibian | T. helveticus | 17 | -0.6 | ‹0.02 | — | Breeding | Beebee 1995 |
| Amphibian | Bufo calamita | 17 | -0.71 | ‹0.01 | — | Breeding | Beebee 1995 |
| Amphibian | Rana kl. esculenta | 17 | -0.58 | ‹0.05 | — | Breeding | Beebee 1995 |
| Amphibian | Rana temporaria | 18 | ? | ‹0.05 | + | Breeding | Forchhammer et al. 1998 |
| Bird | Ardea herodias | 13 | -0.24 | 0.09 | — | Spring Arrival | Bradley et al. 1999 |
| Bird | Monothrus ater | 14 | 0.27 | 0.05 | + | Spring Arrival | Bradley et al. 1999 |
| Bird | Caprimulgus vociferus | 17 | -0.3 | 0.02 | — | Spring Arrival | Bradley et al. 1999 |
| Bird | Sialia sialis | 18 | 0.004 | 0.79 | + | Spring Arrival | Bradley et al. 1999 |
| Bird | Passarella iliaca | 18 | 0 | 0 | 0 | Spring Arrival | Bradley et al. 1999 |
| Bird | Hylocicia mustelina | 20 | -0.08 | 0.22 | — | Spring Arrival | Bradley et al. 1999 |
| Bird | Pipilio erythrophithalamus | 22 | 0.04 | 0.38 | + | Spring Arrival | Bradley et al. 1999 |
| Bird | Ficedula hypoleuca | 22 | -0.39 | 0.07 | — | Breeding | Jarvinen 1989, 1994, 1996 |
| Bird | Ceryls alcon | 23 | -0.09 | 0.17 | — | Spring Arrival | Bradley et al. 1999 |
| Bird | Ficedula hypoleuca | 23 | -0.58 | ‹0.01 | - | Breeding | Slater 1999 |
| Bird | Parus major | 23 | ? | 0.33 | - | Breeding | Visser et al. 1998 |
| Bird | Troglodytes aedon | 24 | -0.34 | 0 | - | Spring Arrival | Bradley et al. 1999 |
| Bird | Turdus migratorius | 25 | -0.24 | 0.01 | - | Spring Arrival | Bradley et al. 1999 |
| Bird | Sturnella magna | 25 | -0.09 | 0.15 | - | Spring Arrival | Bradley et al. 1999 |
| Bird | Bucephala clangula | 25 | -0.64 | 0.006 | - | Breeding | Ludwichowski 1997 |
| Bird | Parus major | 25 | -0.49 | 0.01 | - | Hatch date | Winkel and Hudde 1997 |
| Bird | Parus caeruleus | 25 | -0.46 | ‹0.05 | - | Hatch date | Winkel and Hudde 1997 |
| Bird | Ficedula hypoleuca | 25 | -0.53 | ‹0.01 | - | Hatch date | Winkel and Hudde 1997 |
| Bird | Pheucticus ludovicianus | 26 | -0.4 | 0 | - | Spring Arrival | Bradley et al. 1999 |
| Bird | Sitta europaea | 26 | -0.56 | ‹0.01 | - | Hatch date | Winkel and Hudde 1996 |
| Bird | Branta canadensis | 27 | -0.54 | 0 | - | Spring Arrival | Bradley et al. 1999 |

| Taxa | Species | Years | r | P | Sign | Change | Citation |
|---|---|---|---|---|---|---|---|
| Bird | *Scolopax minor* | 27 | -0.14 | 0.05 | - | Breeding | Bradley et al. 1999 |
| Bird | *Aphelocoma ultramarina* | 27 | -0.15 | 0.05 | - | Breeding | Brown et al. 1999 |
| Bird | *Parus major* | 27 | -0.3 | 0.003 | - | Breeding | McCleery and Perrins 1998 |
| Bird | *Sayornis phoebe* | 28 | -0.38 | 0.09 | - | Spring Arrival | Bradley et al. 1999 |
| Bird | *Toxostomum rufum* | 28 | -0.02 | 0.46 | - | Spring Arrival | Bradley et al. 1999 |
| Bird | *Cardinalis cardinalis* | 29 | -0.22 | 0.01 | - | Breeding | Bradley et al. 1999 |
| Bird | *Agelaius phoeniceus* | 30 | -0.15 | 0.04 | - | Spring Arrival | Bradley et al. 1999 |
| Bird | *Icterus galbula* | 30 | -0.09 | 0.11 | - | Spring Arrival | Bradley et al. 1999 |
| Bird | *Tachycineta bicolor* | 30 | -0.64 | 0.001 | - | Breeding | Dunn and Winkler 1999 |
| Birds | Unspecified | 30 | ? | ‹0.05 | 55 - | Spring Arrival | Sparks 1999, Mason 1995 |
| Birds | Unspecified | 30 | ? | ›0.05 | 91 - | Spring Arrival | Sparks 1999, Mason 1995 |
| Birds | *Miliaria calandra* | 50 | ? | ? | ? | Spring Arrival | Forchhammer et al. 1998 |
| Birds | *Pica pica* | 50 | ? | ? | ? | Spring Arrival | Forchhammer et al. 1998 |
| Birds | *Phylloscopus collybita* | 50 | ? | ? | ? | Spring Arrival | Forchhammer et al. 1998 |
| Bird | *Alauda arvensis* | 51 | ? | ? | + | Spring Arrival | Forchhammer et al. 1998 |
| Forb | *Apocynum androsaemifolium* | 10 | -0.02 | 0.69 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Anemone quinquefolia* | 10 | -0.01 | 0.74 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Oxalis violacea* | 11 | 0.01 | 0.82 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Erigeron strilgosus* | 12 | 0.01 | 0.77 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Linaria vulgaris* | 12 | 0.01 | 0.23 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Pentstemon gracilis* | 13 | 0.00 | 0.39 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Asclepias incarnata* | 15 | -0.51 | 0.00 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Achillea millefolium* | 15 | 0.02 | 0.16 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Viola pedata* | 15 | 0.03 | 0.52 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Hypericum perforatum* | 16 | -0.00 | 0.89 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Lithospermum canescens* | 16 | 0.24 | 0.06 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Asclepias syriaca* | 17 | -0.29 | 0.02 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Anemone patens* | 19 | -0.15 | 0.11 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Uvularia grandiflora* | 19 | -0.09 | 0.22 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Campanula rotundifolia* | 19 | 0.01 | 0.64 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Euphorbia corollata* | 20 | 0.03 | 0.47 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Phlos philosa* | 21 | -0.13 | 0.10 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Phlox divaricata* | 22 | -0.32 | 0.01 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Dodecatheon media* | 22 | -0.23 | 0.02 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Caltha palustris* | 22 | -0.13 | 0.10 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Anemone canadensis* | 23 | -0.17 | 0.05 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Lupinus perennis* | 23 | -0.09 | 0.16 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Rosa Carolina* | 23 | 0.01 | 0.63 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Sisryinchium campestre* | 23 | 0.04 | 0.36 | + | Flowering Date | Bradley et al. 1999 |
| Forb | *Rudbeckia hirta* | 24 | -0.17 | 0.04 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Geranium maculatum* | 24 | -0.02 | 0.51 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Antennaria neglecta* | 24 | -0.01 | 0.67 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Trillium grandiflorum* | 25 | -0.70 | 0.20 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Baptisia leucantha* | 25 | -0.41 | 0.00 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Asclepias tuberosa* | 25 | -0.41 | 0.00 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Aquilegia canadensis* | 25 | -0.26 | 0.01 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Amelanchier laevis* | 25 | -0.04 | 0.33 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Tradescantia ohiensis* | 26 | -0.12 | 0.08 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Dicentra cucullaria* | 28 | -0.07 | 0.19 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Hepatica acutiloba* | 31 | -0.14 | 0.04 | - | Flowering Date | Bradley et al. 1999 |
| Forb | *Linnaea borealis* | 44 | -0.45 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Primula officinalis* | 45 | -0.34 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Oxalis acetosella* | 47 | -0.38 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Trientalis europaea* | 47 | -0.17 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Epilobium angustifolium* | 49 | -0.44 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Caltha palustris* | 49 | -0.40 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Calluna vulgaris* | 49 | 0.05 | ‹0.05 | + | Flowering Date | Post and Stenseth 1999 |
| Forb | *Anemone hapatica* | 50 | -0.60 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Anemone nemorosa* | 50 | -0.60 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Convallaria majalis* | 50 | -0.52 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Tussilago farfara* | 50 | -0.43 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Forb | *Vaccinium myrtillus* | 50 | -0.43 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Tree | *Robinia pseudoacacia* | 12 | ? | ? | ? | Flowering Date | Walkovsky 1998 |
| Tree | *Prunus virginiana* | 18 | 0.15 | 0.11 | + | Flowering Date | Bradley et al. 1999 |
| Tree | *Betula odorata* | 50 | -0.24 | ‹0.05 | - | Flowering Date | Post and Stenseth 1999 |
| Vacular plants | Unspecified | ? | ? | ? | ? | Flowering Date | Menzel and Fabian 1999 |

Includes taxa of the species examined, scientific name of the species, number of years spanned by the data, correlation coefficients (when provided or information available to calculate the coefficients in the citation), P value of the correlation coefficients (when provided in the citation), sign of the relationship between species trait and year, type of change observed, and citations. An unknown value is indicated by "?". (Root et al., 2001.)

number of these associations indicating an earlier phenological shift compared to all reported associations. The phenologies of 94 out of 105 species were recorded as shifting earlier in time. The probability that an estimated phenological shift is earlier, based on a sample size of 13 years, was found to be 0.895 (with a population-wide correlation coefficient of -0.36).

For the meta-analysis of plants showing a change in their blooming or budding dates, the common correlational "fingerprint" for the 48 species from North America and Europe is -0.26, which is statistically different from zero ($P < 0.05$, 95% confidence interval $-0.31 \leq r \leq -0.20$). Again, a strong pattern of consistent shifting toward earlier spring activities is occurring in species of plants investigated.

Numerous studies examined shifts in density, which can be created by a change in abundance within the range of a species, a shift in the range boundary, or both. To test for an underlying pattern using the data available the "vote counting" method was used. For animals and plants, about 200 species show a change in density, with approximately 160 of these changes in the expected direction. The meta-analysis indicates that there is statistically significant movement in the direction expected for these species. While "vote-counting" is often insensitive to detecting underlying effects, the strength of this result indicates that there is most likely a fingerprint in the shifts of densities in both plants and animals.

Results from most studies using long-term data sets provide circumstantial (e.g., correlational) evidence about the association between changes in climate-related environmental factors and animal traits. Circumstantial evidence, insufficient for "proving" causation by itself, is highly suggestive when numerous studies, examining many different taxa from several different locations, are found to be consistent with one phenological fingerprint. Unfortunately, other changes seen in species that are apparently associated with climate change, such as morphological shifts, do not lend themselves as easily to quantification. This does not mean that changes in traits are not shifting in concert. Indeed, about 80% of the species showing change are changing in the manner expected based on species' physiological tolerances (Table OV.1). The Working Group II IPCC TAR authors examining the results of the Root et al. (2001) study concluded that many animals and plants are already responding in concert with the increase in global average temperature of 0.6°C (Summary for Policymakers and Chapter 5, IPCC 2001b).

Meta-analyses provide a way to combine results, whether significant or not, from various studies and find an underlying consistent shift, or fingerprint, among species from different taxa examined at disparate locations. Hence, for studies meeting the strict criteria used by Root et al. (2001), the balance of evidence suggests that a significant impact from climatic warming is discernible in the form of long-term, large-scale alteration of several animal and plant populations. (Note that no claim is made that most plants and animals have been or will be affected by warming. Although that is possible, data are insufficient to show that. Rather, the high confidence conclusion is that many systems are already affected, and the number and scale of the changes will increase with further warming.) The "balance of evidence" conclusion is extended by IPCC (2001b) to include "environmental systems"—sea and lake ice cover and mountain glaciers in addition to the plant and animal taxa examined by Root et al. (2001). Taken together, the IPCC concluded with "high confidence" that the consistent broad-scale pattern of changes observed strongly suggests that a warming of the globe is the most likely explanation of these observed phenomena. Thus, the "discernible statement" of IPCC (1996a) for detection of an anthropogenic climate signal is broadened in IPCC (2001b) to include a "discernible statement" about observed global climatic changes affecting environmental systems. Clearly, if such climatic and ecological signals are now being detected above the background of climatic and ecological noise for a 20th century warming of only 0.6°C, it is likely that the expected impacts on ecosystems of changes up to an order of magnitude larger by A.D. 2100 could be dramatic.

## Climate Forecasts, Ecosystem Responses, and Synergistic Effects

### 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 may be affected. 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.

## *Abrupt Climatic Changes*

We have argued that sustained globally averaged rates of surface temperature change from the past Ice Age to the present were about 1°C per 1000 years (and the large changes in ice masses also occurred on time scales of thousands of years). Alarmingly, a change of a few degrees Celsius per millennia is a factor of 10 or so slower than the expected changes of several degrees Celsius per 100 years typically projected for the 21st century due to human effects. We emphasize the words sustained globally averaged because comparably rapid variations have occurred, at least regionally. 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 hundreds of 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, dramatic shifts occurred outside of the North Atlantic Region (e.g., Severinghaus and Brook 1999), but no comparable 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? The potential for this is speculative, of course, but its possibility has concerned many scientists (Broecker 1994, Rahmstorf 1999). The prospect of climatic surprises in general is concerning 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.

If the complexity of the coupled climate–ecological system is daunting, then recognition of what we actually will experience is even more so. That is, the actual system to be simulated is the coupled physical, biological, and social systems in which human behavior causes disturbances that propagate through natural systems and create responses that, in turn, feed back on human behavior in the form of policies for adaptation or mitigation to the human-induced disturbances. In fact, some very recent studies (e.g., Mastrandrea and Schneider 2001) show that when the socio-natural system is integrated over several hundred years—the time scale of overturning in the oceans—emergent properties can be uncovered. These properties would be difficult if not impossible to find by studying any of the sub-systems in disciplinary isolation. The search for emergent behaviors of complex coupled multicomponent systems will be a primary challenge for the next generation of scientists interested in climate and wildlife connections and their management implications (Kinzig et al. 2000).

## 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 2020s, may not help them adapt to the evolving climate change in the 2030s, 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, Easterling, and Mearns 2000). 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.

The capacity of a system to adapt is a function of the exposure and sensitivity to climate change, as well as the knowledge, infrastructure, and resources available to each adaptive agent. This in turn depends on the social and economic status of each sector or region. Thus the very development conditions that determine how much greenhouse gas is emitted by future society also helps to determine how vulnerable each sector might be to the climate changes so created. Ecosystems, of course, have no capacity to anticipate anthropogenic climate changes nor to deploy a host of technological defenses. That is why most assessments (e.g., IPCC 2001b) continue to claim that human systems are likely to be more adaptable than most natural systems to climate change, at least if there is some foresight as to what changes might occur.

## *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. Recent assessments, fortunately, are beginning to grapple with the difficult problem of variability changes and consequent impacts (e.g., IPCC 2001a, b).

## *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 (e.g., the Vegetation/Ecosystem Modeling and Analysis Project 1995). What is needed for more realistic and useful

ecological impact assessments is a multiscale, multispecies, multi-taxa analysis driven by regionally specific, transient climate change forecasts. The construction of ecological forecast models first requires large-scale data sets gathered locally by professional (e.g., U.S. Geological Survey land-cover data sets) and volunteer (e.g., 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 and testing with both large- and small-scale data sets to more credibly address the cross-scale and multicomponent problems of ecological assessment—another instance of what we (Root and Schneider 1995) have labeled SCS. The SCS paradigm has two motivations: (1) better explanatory capabilities for multiscale, multicomponent interlinked environmental (e.g., climate–ecosystem interactions or behavior of adaptive agents in responding to the advent or prospect of climatic changes) and (2) more reliable impact assessments and problem-solving capabilities—predictive capacity—as has been called for by the policy community.

Finally, to mobilize action to mitigate potential risks to environment or society, it is often necessary to establish that a discernible trend has been detected in some variable of importance (e.g., the first arrival of a spring migrant or the latitudinal extent of the sea ice boundary) and that the trend can be attributed to some causal mechanism (e.g., a warming of the globe from

increases in anthropogenic greenhouse gases). Pure association of trends in some variables of interest are not, by themselves, sufficient to attribute any detectable change above background noise levels to any particular cause. Explanatory mechanistic models are needed, and the predictions from such models should be consistent with the observed trend before a high confidence can be assessed that a particular impact can be pinned on any suspected causal agent. We have argued that conventional scaling paradigms—top-down associations among variables believed to be cause and effect; bottom-up mechanistic models run to predict associations but for which there is no large-scale data time series to confirm—are not by themselves sufficient to provide high confidence in cause and effect relationships embedded in integrated assessments. Rather, we suggested that a cycling between top-down associations and bottom-up mechanistic models is needed. Moreover, assessors cannot assign high confidence to cause and effect claims until repeated cycles of testing are done in which mechanistic models predict outcomes and large scale data "verifies" that these mechanistic models are at least partially explanatory. Very high confidence usually requires a considerable degree of convergence in the cycling between top-down and bottom-up components, as well as sufficient baseline data for testing over long periods. We believe there are a number of taxa that have already demonstrated likely responses to regional-scale climatic changes over the past century, and that these responses are fairly coherent over widely separated geographical regions (see the Summary for Policymakers and Chapter 5 of IPCC 2001b, Parmesan et al. 2000, Sagarin this volume, Crozier this volume, and Root et al. 2001). Taken together, the consistent broad-scale pattern of changes observed strongly suggests a warming of the globe to be the most likely explanation of these observed phenomena, although for the reasons given in the above sentences, we would not yet assign a very high confidence to that inference. The efforts of the NWF authors in this volume are examples of the kinds of studies that will be needed to further increase our confidence in the recognition that climate change and other human disturbances not only have the potential to alter wildlife patterns significantly and create serious stresses for vulnerable species, but that this process has already begun and can be demonstrated with a disturbingly high level of confidence.

# Notes

1. The numerical results for the meta-analyses (generally in parenthesis) were the values used for the IPCC, Working Group II, Third Assessment Report (IPCC 2001b). The actual numbers in Root et al. (2001) may differ owing to the ongoing review process.

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