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## Biological Impacts of Climate Change

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*Ok, so you convinced me that global warming is happening, but why should my constituents care?*

*Anonymous U.S. Congressional Staffer, 2004*

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Global climate is swiftly changing, with poorly known consequences for biodiversity and human well being. In the last 90 years Earth's mean temperature rose 0.6°C, a rate of increase that has not been seen in 10,000 years. Since the mid-1990s, it has been clear that mean global temperature rose during the twentieth century, but for several more years the cause of the observed warming was much debated in scientific circles. The United Nations and the World Meteorological Organization perceived that if humans were causing a fundamental shift in global climate, the consequences could be enormous for all peoples. To facilitate reaching a global scientific consensus, the Intergovernmental Panel on Climate Change (IPCC) was formed, whose Third Assessment Report (IPCC 2001a) involved more than 1200 scientists from diverse disciplines. The consensus among the more than 200 climate experts from IPCC Working Group I was that "global rises in mean yearly temperature of the past 50 years were primarily due to global rises in anthropogenically produced greenhouse gases" (i.e., carbon dioxide, methane, nitrous oxide, and halocarbons) and that the rate of temperature change will itself accelerate over the coming century (IPCC 2001a).

As with many other conservation issues, however, the most influential debates—those in the policy and public arenas—continue well beyond the point of scientific consensus. And, indeed, consensus on the cause of global warming is only the beginning of a series of new questions. What does anthropogenic climate change signify for the future? Is climate change a reversible process, and how quickly will new weather patterns emerge? What can be done to mitigate the detrimental effects of altered climates? How will new climatic patterns influence species and ecosystems already besieged by other human-induced pressures?

Signs of climate change are already visible, although most effects have been relatively mild compared to other anthropogenic threats to wild species, particularly habitat loss and degradation. Conservation concerns about climate change are less focused on current impacts or even on impacts over the next decade but on consequences from 50 to 100 years from now. Existing climate models predict widespread

and dramatic alterations in weather patterns over coming centuries, altering all nations and virtually every ecosystem. In the long term, climate change is likely to rise to the forefront of threats to biodiversity and endangered species. The scale, duration, and probable severity of climate change separate it from other environmental issues. Indeed, national and international political responses to the challenge of climate shifts has been more comparable in scale to preventing HIV/AIDS or polio than strategies to counteract local or regional issues such as species invasion or overexploitation. Climate change is the one threat that exists everywhere, cannot be reversed by local actions, and will continue even if all nations come to agreement to tackle the problem.

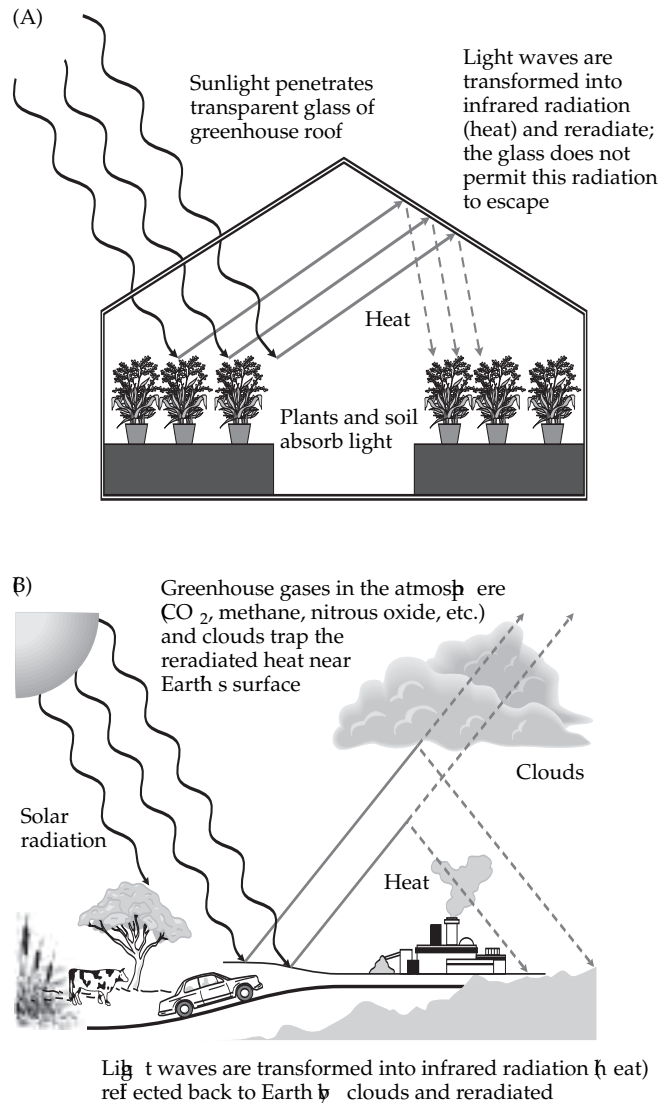
In this chapter, we shall discuss some basic processes that have shaped climate in the past and how those processes have been altered during the twentieth century, the relationship between climate, wild species, and ecosystems, and the conservation implications of long-term climate shifts. Finally, since climate change has been defined as a global threat as well as a regional and local issue, we will discuss international climate change policy with special attention to the United States and Canada.

## The Nature of Climate Change

Generally speaking, climate shifts have been caused by changes in the retention and distribution of solar energy across the planet. Solar radiation passes through the atmosphere as short wavelength ultraviolet (UV) waves. When UV waves hit Earth's surface, they are transformed into long wavelength infrared (IR) waves, which we perceive as heat (Figure 10.1). A remarkable aspect of Earth's biosphere is that a system has developed that has been able to maintain sufficient quantities of life-promoting liquid water for billions of years. Such a system implies a relatively stable pattern of energy retention.

The atmospheric gases that are most important in maintaining Earth's current energy balance are carbon dioxide ( $\text{CO}_2$ ), methane ( $\text{CH}_4$ ), and water vapor, gases that cannot be penetrated by radiation in the infrared spectrum. These gases are referred to (with more poetic license than accuracy) as "greenhouse gases" by analogy to the glass of a gardener's greenhouse. Short-wave (UV) energy is allowed to pass through our atmospheric window, but the transformed long-wave (IR) energy is prevented from dissipating back into space.

Greenhouse gases are really more like a blanket surrounding and insulating Earth's surface. The resulting greenhouse effect maintains our relatively stable surface temperatures. Natural levels of Earth's greenhouse gases maintain temperatures about  $60^\circ\text{F}$  above what it would be if Earth's atmosphere lacked such gases. In contrast

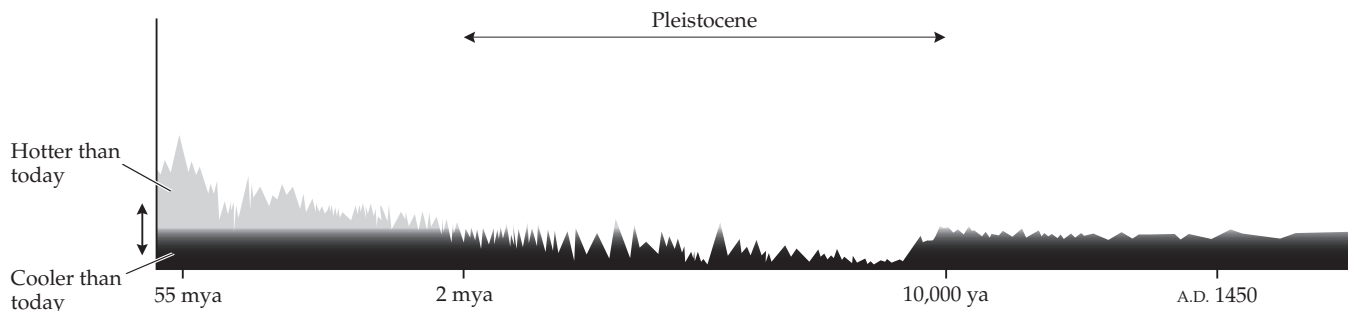


**Figure 10.1** The greenhouse effect. Earth's atmosphere already serves as a greenhouse that warms Earth's surface (A), but human influences are increasing this effect (B). About 70% of UV wavelengths pass through Earth's atmosphere, whereas about 30% are reflected. Burning of fossil fuels in industry, automobiles, and buildings, as well as deforestation give off  $\text{CO}_2$  to the atmosphere that enhance the greenhouse effect. In addition, methane from swamps, rice paddies, and cattle enter the upper atmosphere and trap heat. (From Primack 2004.)

this natural greenhouse effect, any temperature increase attributable to human activity is referred to as the **enhanced greenhouse effect**.

### Climate change through the ages

Since the industrial revolution, burning of coal, oil, and natural gas has increased levels of greenhouse gases by about 30%. Mean global temperatures increased  $0.6^\circ\text{C}$



**Figure 10.2** Average global temperature over the last 65 million years. Gray indicates temperatures hotter than today; black indicates temperatures cooler than today. At 65–100 million years ago (mya; the age of the dinosaurs), CO<sub>2</sub> was much higher than it is today and the climate was much warmer and wetter. About 13 million years ago, we start to see brief periods in which temperature and CO<sub>2</sub> levels were as high as they are today. The Pleistocene period began around 2 mya and ended 12,000 years ago, during which Earth cycled between glacial (frozen) and interglacial (warm) periods. Note that climate had been relatively stable over the past 10,000 years. (Modified from *National Geographic*, May 1998.)

between 1860 (when collection of accurate temperature records began) and 1998 (IPCC 2001a). Based on what is known about the properties of these gases, it has long been clear that they would have some effect on Earth's climate system. Early in the 1990s, however, it was unclear how much of the observed temperature rise was due to the rise in greenhouse gas concentrations as compared to natural variation in climate.

Investigations of global climate change, Earth's climatic history, and the many causes of climate fluctuation have been actively pursued for over a century. Putting a 0.6°C temperature rise into appropriate context requires an analysis of climate change at several scales and an appreciation of the impermanence of "normal" climate.

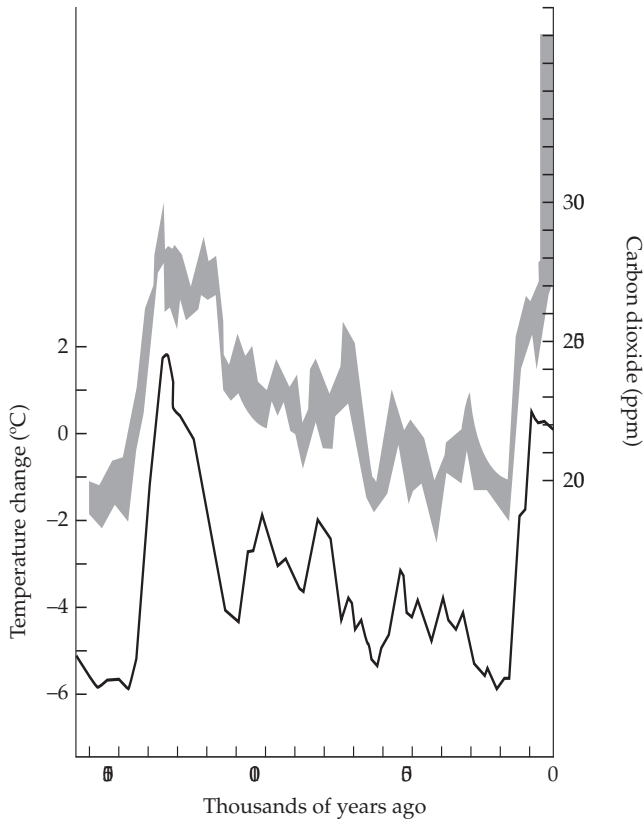
Climate certainly shows natural variation, even at time scales shorter than an average human lifespan. However, short-term variation is not a reliable indicator of long-term climate trends. Indeed, there is much confusion over the contrast between weather (which refers to a specific event or a brief period, such as a thunderstorm or a spring with low rainfall) and climate (which refers to long-term averages, such as the amount of rain that can be expected to fall during an average monsoon season in Mumbai, India). Climate trends are not visible in particular weather events but can be deduced over many weather events. An especially mild winter in New England cannot be "blamed" on human-induced factors. But a trend between 1950 and 2000 for shorter and milder winters in New England could be reasonably ascribed to a climate shift.

Indeed, Earth's climate has varied significantly enough for the definition of "normal" global climate to differ sub-

stantially based on the observer's time scale. Planetary temperatures appear to have begun trending downward since the beginning of the Tertiary period, starting between 50 and 60 million years ago (mya) and falling by 10°C. Today's climate, then, is relatively cool at this level of resolution (Figure 10.2).

Finer scales make different patterns apparent. Using data from ocean sediment cores, coral reef cores, and other paleoecological data, one can see fluctuations in surface temperatures since the end of the Cretaceous. During the geologically recent Pleistocene (a period that lasted between 1.8 million to 12,000 years ago), global climate exhibited large-scale periodic fluctuations in temperature and precipitation. These fluctuations—the Milankovitch cycles—match changes in Earth's orbit and tilt relative to the sun's axis that subtly alter the amount, location, and timing of solar energy reaching Earth (Imbrie and Imbrie 1986). The strength and speed of temperature change is believed to be driven by a series of positive and negative feedbacks through the biotic and abiotic systems, with greenhouse gas concentrations being the strongest driver.

There is a strong correlation between greenhouse gas abundance and mean temperatures. For instance, cores drilled in the Arctic and Antarctic ice sheets contain tiny air bubbles embedded when the ice formed. These bubbles reveal the exact composition of the atmosphere at the time of ice deposition. Not only does this give an exact value for atmospheric carbon dioxide levels, but scientists have discovered that the ratio of two isotopes of oxygen (<sup>18</sup>O<sub>2</sub> and <sup>16</sup>O<sub>2</sub>) can be used to accurately calculate atmospheric temperatures at the time the ice was



**Figure 10.3** The relationship between temperature (normalized to today's average global °C), and carbon dioxide (ppm) over the past 160,000 years. Ice core samples show a clear correlation between atmospheric CO<sub>2</sub> concentrations (gray line) and the global temperature record (black line). Note that the current level of CO<sub>2</sub> (at 360 ppm) is far higher than the highest natural level. (Modified from IPCC 2001a.)

formed. Using data from various locations (Greenland, Siberia, and Antarctica), a record of greenhouse gas composition extending back 740,000 years has been assembled, with much of this span resolvable to individual years (McManus 2004). Over this period, carbon dioxide levels and mean global temperatures are closely correlated (Figure 10.3; IPCC 2001a).

Estimates from geological evidence show that carbon dioxide in the atmosphere during the peak of the Cretaceous was much higher than now. There are two major reasons why these levels declined, one biological and one geological. The Cretaceous was a time in which terrestrial plants expanded and thrived. However, wet, anoxic conditions slowed decomposition and dead plant matter built up in large quantities. Subsequent burial and exposure to massive pressures transformed these dead organic deposits into coal and oil formations. Thus, the Cretaceous was a time in which the terrestrial plant biome was a huge carbon sink (i.e., living plants took up

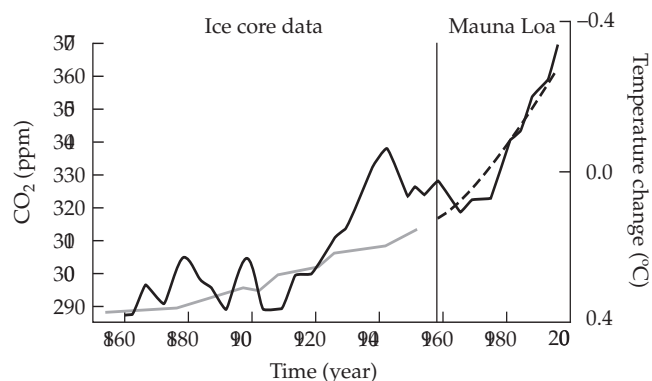
more carbon dioxide than was released through decomposition), and much of the atmospheric carbon dioxide left over from early in Earth's history became stored as what we now call "fossil fuels." After the major extinction event at the end of the Cretaceous Period, in which 76% of species went extinct, the following Tertiary Period was characterized by another massive evolutionary radiation of terrestrial plant species. Trees became dominant at this time, with tall dense forests spreading over much of the land—their wood draining the atmosphere of another large pool of carbon. Finally, at this time vast limestone deposits were formed. Carbon is a major component of limestone. Thus, over several million years, vast quantities of carbon were sucked out of the atmosphere and put into long-term storage ("sequestered") in the form of oil, coal, natural gas pockets, stands of forest, and rock formations.

The more recent temperature changes in the Pleistocene can help us understand how much of a shift in temperature is necessary to affect major physical and biological features of Earth. Pleistocene climates alternated between two extremes: glacial (cold and dry) and interglacial (warm and wet) periods. Average Pleistocene temperature cycling from the beginning of a glacial period to the end of an interglacial period operated on a scale of about 100,000 years. Peak glacial periods were about 5°C cooler than current global mean temperatures, which is substantial enough a decrease for glaciers to cover the majority of the Northern Hemisphere and for sea levels to be several hundred meters lower than current levels. Increasing global temperatures will push our current climate pattern (interglacial) to one that is warmer than any sustained period during the Pleistocene—or indeed over the past 10 million years.

### **Human enhancement of the greenhouse effect**

The insulating properties of carbon dioxide were discovered in the mid-1800s. The greenhouse effect as a major driver of Earth's climate system was first hypothesized by Svante Arrhenius in 1896. He even predicted that the emission of carbon dioxide by combustion of coal following the advent of the Industrial Revolution (about 1750) would eventually warm the world (Weart 2003).

Our contemporary climate represents the end of an interglacial period. For unknown reasons, glacial–interglacial cycling stopped about 10,000 years ago and temperatures have remained relatively stable, varying by only 1°C (see Figure 10.2). Over that time, atmospheric carbon levels shifted only about 10% until the Industrial Revolution. Therefore, the increase of 0.6°C since 1910 represents a large and sudden change compared to natural variations over the past 10,000 years. Further, atmospheric carbon dioxide levels rose 36% since 1910—from 280 ppm to 380 ppm—which is significantly outside the



**Figure 10.4** Relationship between twentieth century levels of atmospheric carbon dioxide and global temperature. The solid gray line shows CO<sub>2</sub> records from ice cores, the dashed black line shows annual average CO<sub>2</sub> records from atmospheric measurements in Hawaii, and the black line shows mean yearly global temperature trends. This steady increase of CO<sub>2</sub> in the atmosphere has caused greater retention of heat and a gradual warming of Earth. (Modified from IPCC 2001a.)

bounds of natural variability over the past half million years (see Figure 10.3). Like withdrawing money long stored in a huge bank vault, the Industrial Revolution has allowed these carbon deposits to once again circulate in the world's "carbon economy."

There is now a strong consensus among climate scientists that Earth's mean surface temperature has increased, and that this heating is largely due to human-induced increases in greenhouse gas concentrations (Figure 10.4; Crowley 2000; IPCC 2001a; Karl and Trenberth 2003). Most of the surface temperature increase is due to the enhanced (rather than the natural) greenhouse effect.

### ***Mechanisms regulating the global energy budget***

Humans actually produce a variety of greenhouse gases, most of which already existed in the atmosphere prior to the Industrial Revolution. Of all the greenhouse gases produced by humans, however, the greatest concern surrounds the production of CO<sub>2</sub>. Not only is CO<sub>2</sub> produced in much greater quantities than any other of the greenhouse gases, but a carbon dioxide molecule remains stable in the atmosphere for over 100 years. In contrast, methane is 100 times stronger than CO<sub>2</sub> in its greenhouse effects, but a methane molecule is broken down in about a decade. Methane is produced in the low-oxygen conditions of rice fields, from the digestive systems of cattle and other ruminants, and as a by-product of coal mining and natural gas use. Most of the remaining greenhouse effect is from nitrous oxides and chlorofluorocarbons (CFCs) (both produced largely by industrial processes) and low-atmosphere ozone (from fossil fuel combustion).

Collectively, all of the activities and processes that increase the ability of Earth's surface and atmosphere to absorb and retain solar energy are referred to as positive radiative forcings. Direct solar radiation and greenhouse gases cause major positive radiative forcing, but others also exist. For instance, deforestation creates positive radiative forcing if it is replaced by grasslands (such as pastures following a clear-cut). Trees cool their locality by high evapotranspiration rates (like an evaporative cooler used in commercial greenhouses). A pasture at the same site has much lower rates of evapotranspiration and will be hotter than a forest on average, everything else being equal.

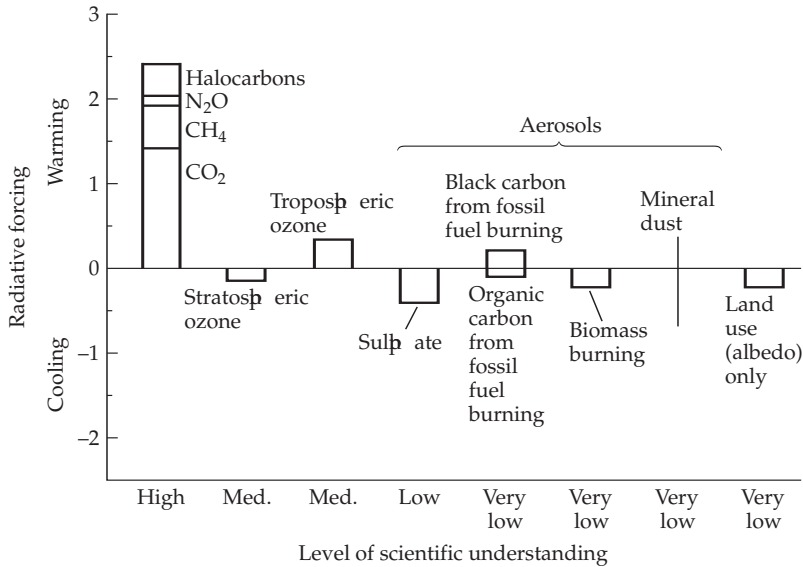
In contrast, negative radiative forcings tend to cool Earth's surface and lower atmosphere. For instance, sulfur dioxide (SO<sub>2</sub>) from car exhaust and industrial processes such as coal-powered electrical plants form aerosols (small particles suspended in the atmosphere) that reflect solar energy back into space and hence cool Earth's surface air temperatures.

Mediating positive and negative radiative forcings is the relative reflectance, or albedo of Earth's surface and clouds. Different surfaces have different albedos. Snow reflects UV and cools surface air temperatures, whereas bare dirt converts UV to heat and warms Earth's surface. Taken together, the interaction of positive and negative radiative forcings and albedo is quite complex. Because SO<sub>2</sub> also causes acid rain, there have been recent attempts in industrialized nations to reduce SO<sub>2</sub> pollution. Because SO<sub>2</sub> remains in the atmosphere for only a week, reduction of SO<sub>2</sub> emissions will immediately lessen its impact as a negative radiative forcing.

Moreover, forcings can have either natural or anthropogenic origins. Mount Pinatubo in the Philippines had a major eruption in 1991 that increased global aerosol concentrations. The ash output contained 25–30 million tons of sulfur dioxide that entered the atmosphere during a very short period and which rapidly dispersed across the globe. Mount Pinatubo temporarily reduced global mean temperatures, though within three years the particulate matter had largely left the atmosphere and global temperatures rebounded to their former levels (Yang and Schlesinger 2002).

The concept of radiative forcing is used to classify and track the cycling of elements and compounds relevant to climate change through meteorological, geological, hydrological, and biological systems. Figure 10.5 shows the latest consensus on the relative contributions of known radiative forces on twentieth century temperature trends.

Much attention has been focused on the carbon cycle because carbon is such an important component in carbon dioxide and methane. The complete carbon cycle consists of carbon "sinks" (processes that remove carbon from atmospheric circulation), and carbon "sources" (processes



**Figure 10.5** Estimates of strengths of radiative forces on global energy budget. Radiative forcing is in watts/m<sup>2</sup>. Positive forces (above zero) warm Earth's surface; negative forces (below zero) cool Earth's surface. (Modified from IPCC 2001a.)

that release stored carbon into the atmosphere). There are numerous sources and sinks for carbon, encompassing both biotic and abiotic systems. While the carbon fluctuations documented by ice cores record the net effect of changes in the relative balance between sources and sinks, these records do not by themselves describe which aspects of the carbon cycle changed. One of the goals of research into the processes behind the carbon cycle therefore is to determine the relative contribution of natural and anthropogenic sources to recent changes in the concentration of greenhouse gases. Current carbon dioxide levels, for instance, could reflect an increase in the output of carbon sources (e.g., due to elevated industrial activity) or because carbon sinks have decreased their input (e.g., due to decreases in the growth rate of tropical rainforests). Such knowledge is vital to predicting greenhouse gas concentrations in the future.

Research into the cycling of other elements and molecules also attempts to untangle the synergies of various systems. For example, water vapor is the most abundant and important of all of the natural greenhouse gases, but its effects are not included in the enhanced greenhouse effect since humans do not produce water vapor in a manner comparable to the other greenhouse gases. Water vapor concentrations are probably increasing, however, as a side effect of rising global temperatures. A warmer atmosphere is able to hold more water vapor, and higher ambient temperatures increase oceanic evaporation and vegetation transpiration rates. The implications of these changes over long time scales are uncertain.

Perhaps the most frightening prospect in this regard is a so-called runaway climate shift, leading to a sudden and large increase or decrease in global temperature. Several researchers modeling periods of climate change in the past suggest that elemental cycles normally oper-

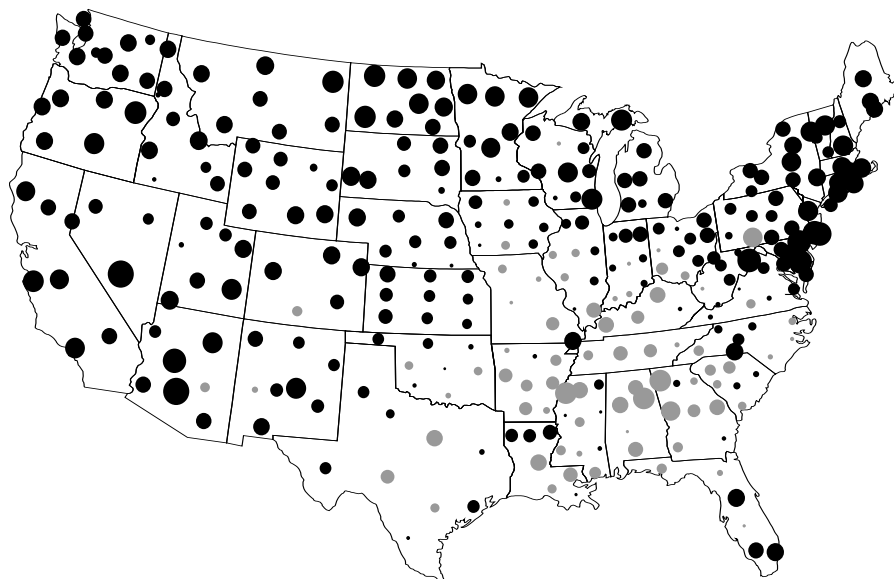
ate within tolerances that allow minor climate variation but that resist significant shifts. However, if some tolerances are exceeded, several radiative forcings may reinforce one another and push global climate through a period of rapid change before reaching a new plateau. For example, if greenhouse gases reached a certain threshold level, then the resulting increased air temperatures may trigger large-scale melting of polar land ice. This would expose dark surface rocks that have been covered for a very long time. These new dark surfaces would absorb more solar energy than the former ice cover, which would spawn additional, rapid large-scale melting.

## Current and Future Climate Change

To predict future climate, scientists have developed and tested **global climate models (GCMs)** based on the processes by which atmospheric greenhouse gases affect global climate. Though there are some differences among models used by, say, the National Center for Atmospheric Research (NCAR) in the U.S. and by the Hadley Center in the U.K., there are also many broad agreements. We review these briefly here.

### Temperature and precipitation changes

All GCMs indicate that greenhouse-gas-driven warming should be greatest at the poles and weakest in the tropics, and this is indeed the pattern seen in recent analyses of global temperature change over the twentieth century (IPCC 2001a). In some parts of Alaska, Canada, and Siberia, mean annual temperatures have increased by 2–4°C since 1900, much more than most areas of the lower 48 states of the U.S. (Oechel et al. 1993; IPCC 2001a). One of the striking trends at mid- and high latitudes has been toward fewer days and nights below freezing in wintertime and more ex-



**Figure 10.6** Temperature trends in the lower United States from 1901 to 1998. Black indicates areas that are warming and gray indicates areas that are cooling. The size of the dot indicates the magnitude of temperature change, with the largest dots representing a change of 3°C per 100 years. (From National Climatic Data Center/NESDIS/NOAA.)

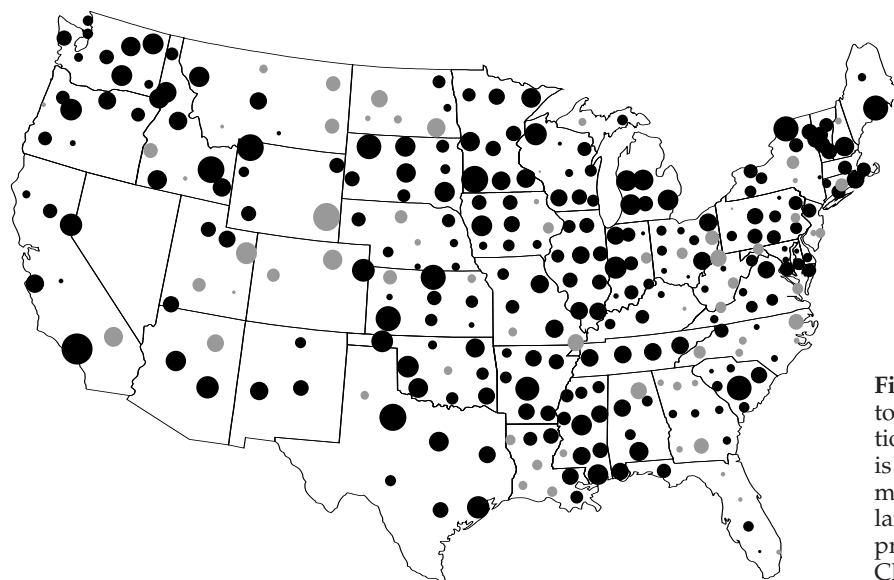
treme heat days in summer. These events may in some cases simply reflect the same level of variation but around a new, higher mean, but there are indications that yearly variance in temperatures has also increased (Karl et al. 2000; Karl and Trenberth 2003).

In the U.S., warming averaged about 0.7°C (1°F) during the twentieth century. New regional models and analyses also conclude that the North American warming trend can largely be attributed to a rise in greenhouse gases (Karoly et al. 2003; Stott 2003; Zwiers and Zhang 2003). Still, there is variation across the U.S., with some areas even cooling (Figure 10.6).

It is becoming increasingly apparent that aspects other than temperature are also changing (reviewed by Meehl et al. 2000a,b; Easterling et al. 2000a,b). Precipitation has

increased globally, and precipitation events have been increasing in intensity. Consequently, major floods have been occurring more frequently and with greater severity (Karl et al. 1996; Karl and Knight 1998; Groisman et al. 1999; IPCC 2001a). In the U.S., total precipitation has increased by 5%–10% over the twentieth century, but there is regional variation. Winter precipitation (snow) has increased in the Great Lakes region, while other U.S. regions are becoming drier (e.g., eastern Montana; Groisman et al. 2001) (Figure 10.7).

Making predictions for coming decades has proven difficult. Even if all human emission stopped immediately, enough greenhouse gases have been added to the atmosphere to sustain temperature increases throughout the twenty-first century. In reality, the emission of all



**Figure 10.7** Precipitation trends from 1901 to 1998. Black indicates areas where precipitation is increasing and gray indicates where it is decreasing. The size of the dot indicates the magnitude of precipitation changes, with the largest dots indicating a 40% change in the precipitation over 100 years. (From National Climatic Data Center/NESDIS/NOAA.)

greenhouse gases (except CFCs and methyl bromide) has continued to rise since 1990, leading to predictions by the IPCC of a quickening in the rate of climate change due to the enhanced greenhouse effect. Indeed, carbon levels now increase about 10% each twenty years, and between 1976 and 2000 global mean temperatures have risen at a rate of 3°C per century.

The need for accurate climate predictions has challenged climate scientists to create increasingly sophisticated computer models to simulate atmosphere dynamics. To develop predictions that would be useful to policymakers, the IPCC (2001a,b) devised four basic “scenarios” to understand warming trends over the twenty-first century. These scenarios are based on different assumptions about global development, population growth, technological improvements in energy conservation and creation, and approaches to the management of greenhouse gas emissions. These scenarios also differ in their target carbon dioxide stabilization level between 450 ppm and 1000 ppm (remember that 1990 levels were 350 ppm). These are further subdivided into a total of 40 scenarios, which are the basis for specific climate models.

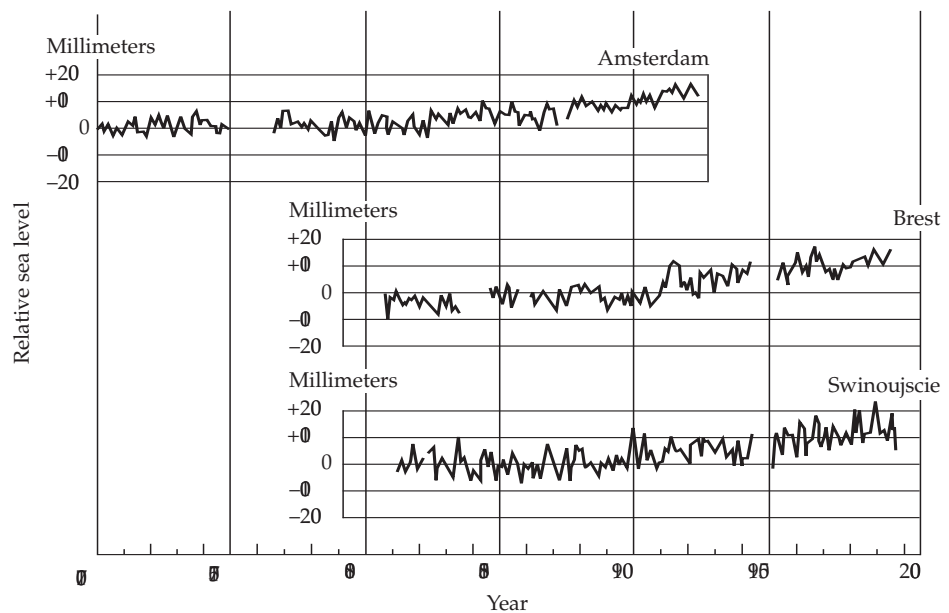
Using 1990 as a baseline, these models predict an increase in global temperature between 1.4°C and 5.8°C by 2100. Other trends are also seen across models. One of the ironies of climate projection to 2100 is that while precipitation is expected to continue to increase, higher air temperatures will lead to more rapid evaporation. Moreover, the increase in variance of precipitation events will change the patterns of water availability (seasonality and frequency), which may be more important to humans and to wildlife and ecosystems than a change in

total amount of precipitation per year. In other words, more rain may fall in a given locality, but the additional rainfall may or may not result in substantially altered ecosystem dynamics. As a further complication, a sustained rise in mean global temperatures is expected to cause changes in global air and ocean circulation patterns that, in turn, will affect regional climates to varying extents (IPCC 2001a,b). All of these processes are very difficult to model, particularly as an evolving system.

### Oceans: Change in sea level and circulation

The boundary between land and water has often moved over time. Twenty thousand years ago for instance, sea levels were about 120 m lower than current levels and glaciers covered much of the Northern Hemisphere. Clearly large shoreline movements are likely to have profound impacts on marine and terrestrial species and ecosystems near coastlines. On shorter time scales, however, variation has usually been small.

Measurements of sea level for the years before the nineteenth century come from geological analyses of rock formations and fossil coral reefs. Global sea level variations have averaged between 0.1 and 0.2 mm annually over the past 3000 years. Since the nineteenth century, shoreline data come from direct measurement of ocean level by tide gauges. These records document that ocean levels have risen over the past 200 years, and that the twentieth century showed a greater increase than the nineteenth (IPCC 2001a) (Figure 10.8). The rate of increase over the twentieth century has averaged between 1 and 2 mm annually, ten times the estimates for the past 3000 years (IPCC 2001a). Several recent studies have linked the



**Figure 10.8** Sea level rise over the past 300 years in three European cities. A limited number of sites in Europe have nearly continuous records of sea level spanning 300 years; these records show that the greatest rise in sea level took place over the twentieth century. Records shown from Amsterdam, The Netherlands, Brest, France, and Swinoujscie, Poland, as well as other sites, confirm the accelerated rise in sea level over the twentieth century as compared to the nineteenth. (From IPCC 2001c.)

observed increase in ocean temperatures and in sea level to rises in atmospheric greenhouse gases (Barnett et al. 2001, IPCC 2001a; Levitus et al. 2001; Reichert et al. 2002; Gillett et al. 2003).

Sea level rise is due both to thermal expansion and to an increase in total water as land ice melts. Thermal expansion is simply the increase in volume of any liquid as it gets warmer. Given the very large total volume of Earth's oceans, a small temperature change can have an important effect. Observations over the twentieth century suggest that thermal expansion is responsible for an average of 1 mm annually (IPCC 2001a). Because liquid water has a much higher heat capacity than the atmosphere, there is a much longer lag time between adding heat to the ocean and observing a temperature rise than there is for warming the atmosphere. If atmospheric carbon dioxide were fixed at current levels, atmosphere temperatures would continue to rise for another 100 years and lagging thermal expansion would cause sea levels to rise for many centuries.

More directly, seas rise from an increase in water. The largest quantity of non-ocean water is locked up in massive polar ice sheets. In geological terms, sudden shifts in sea level have occurred before, as when sea levels rose at an average annual rate of 10 mm per year between 15,000 and 6,000 years ago as glaciers melted and retreated poleward. Melting of the polar ice caps has contributed between 0.2 and 0.4 mm annually to sea level increases over the twentieth century (IPCC 2001a). Sea level rise is predicted to accelerate from the 20–30 cm over the twentieth century and to 35–90 cm over the twenty-first century. (IPCC 2001a). The effects of rising sea levels on ecosystems will be substantial. Coastal areas are expected to suffer increased erosion rates with more severe storm surges associated with higher sea levels.

Major ocean circulation systems are already showing signs of being affected by the rise in atmospheric temperatures. The cyclical shift in Pacific Ocean currents, "El Niño," results in massive warming in the mid-Pacific and a warm tongue of water creeping up the west coast of North America and pushing away the normal cold current that flows from Alaska. An El Niño year is characterized by dryer, warmer conditions in the Pacific Northwest (Oregon and Washington) and much wetter conditions throughout much of California and the Southwest. Major El Niño events, such as the ones in 1982–1983 and 1997–1998, cause substantial flooding. El Niño events have increased in frequency and intensity, and some models predict that the "normal" state by 2050 may resemble "El Niño-like" conditions (Meehl et al. 2000b).

**SNOW, ICE, AND HYDROLOGICAL CHANGES** Dramatic declines in long-term snow and ice cover already have occurred over the past century (IPCC 2001a,b). There has

been a widespread retreat of mountain glaciers in North America, South America, Europe, Africa, New Zealand, and central Asia during the twentieth century. Since 1850, the glaciers of the Swiss Alps have lost about 30%–40% of their surface area and about half of their volume. The permanently snow-capped Mount Kenya and Mount Kilimanjaro in Africa have lost over 60% of their glacial volumes in the last century. In Glacier National Park, glaciers have declined by 70% and are expected to disappear completely by 2020 (Hall and Fagre 2003). It is estimated that about 30% of the projected change in sea level by 2100 will likely come from melting land ice (IPCC 2001a). The shrinking of glaciers will also have significant socioeconomic impacts. Many areas depend on permanent snowpack to keep their reservoirs filled through the summer. Rapidly melting glaciers increase rock and ice falls, which lead to high rates of erosion. Moreover, the loss of scenic beauty will likely affect areas heavily dependent on tourism (Figure 10.9).

Flood events result in more rain disappearing as runoff rather than soaking into the ground. As a result of predicted increased flooding in many regions, soil moisture may decline and underground aquifers many have longer recharge periods. Clearly, freshwater hydrology could alter substantially, but variably, across the globe.

Climate scientists have been modeling the combination of these effects on relatively large scales. For instance, most rain in western California occurs in the winter, and summer river flow is largely derived from the gradual melting of the Sierra Nevada alpine snowpack. But winter snowpack is changing, with trends toward lighter snowpack and earlier melt date at lower elevations and heavier snowpack at higher elevations (Johnson et al. 1999). Current models suggest that winter



**Figure 10.9** Worldwide, glaciers are retreating. Here date signs show the retreat of the Exit Glacier in the Kenai Peninsula, Alaska. (Photograph © Y. Momatiuk/Photo Researchers, Inc.)

alpine temperatures will increase enough to lower total snow accumulation in mountain regions of the U.S. (U.S. National Assessment Report 2001). The increased precipitation will instead fall as rain, causing western slope streams and rivers to have stronger winter flows relative to spring and reducing summertime flow substantially.

Recent studies of nonregulated streams in the U.S. showed the initial signs of these changes: Peak spring flow had advanced by about two to three weeks since the 1950s (Lins and Slack 1999; Groisman et al. 2001). In mountainous regions, this shift has been related to earlier melting of winter snowpack (Dettinger and Cayan 1995; Johnson et al. 1999). Shifts in hydrological trends are likely to alter local freshwater and terrestrial ecosystems and necessitate major adjustments in the current regime of human water use.

In some cases, managed freshwater systems may be buffered against climate change in regions with strongly regulated flow regimes via canalization of streams and building dams. However, these engineering solutions come at a cost to native biodiversity. For example, dams along the Columbia River in the northwestern U.S. have been shown to impede upstream migration of adult salmon as well as downstream migration of their offspring. Dams are considered a primary reason why Pacific salmon have failed to recover even after fishing was greatly reduced. At a time when conservation biologists are arguing for dam removal, the consequences of climate change for water availability may bring about greater pressure to build dams to maintain water for urban and agricultural areas.

## Predicted Biological Impacts

Concern about the conservation implications of climate change stems from a substantial body of literature that affirms the importance of climate in shaping natural systems. Over a century of ecological research demonstrates the crucial role of climate in determining the systematic geographical patterns in the distribution of major biomes or vegetation communities (Woodward 1993). In turn, the distributions of the animals associated with and dependent on these vegetation communities are also a function of climate (Andrewartha and Birch 1954).

Biologists use multiple approaches to form projections of ecological changes expected to accompany various types of climatic change. Predictions of how ecological systems and species may “behave” in response to climate change come from snapshot analyses of current relationships between climate contours and species’ distributions (their “**climate envelope**”), from manipulative laboratory studies on plant and animal physiologies with respect to temperature and precipitation tolerances, and from analyses of the fossil record. Most studies seek

to predict how particular species will react to climate change, and increasingly, conservationists are seeking to predict how interacting webs of species might change (for an in-depth discussion of these complexities see Case Study 10.1 by Lisa Crozier).

During the great Pleistocene glacial–interglacial cycles, the world experienced much more dramatic climatic changes than were seen during the twentieth century (detailed previously). Massive range shifts and some extinctions occurred (Huntley 1991; Davis and Zabinski 1992; Coope 1995). Over time, ecosystems adjusted to climate changes and new types of communities emerged across the landscape.

Using fossil evidence to predict ecosystem responses to current warming trends, one might first assume that ecosystems will move to new locations that are relatively similar to their current abiotic limits given new climatic constraints. Thus, a marine kelp forest might gradually shift its location to a cooler (and deeper) zone, or a large coastal salt marsh might move inland and higher in elevation as sea levels rise. Such simple movement of ecosystems may be unlikely in most cases, however. Studies of individual members of complex ecosystems show that each species tends to have different environmental needs and tolerances. Some members of the ecosystem may move and others may have no clear path for retreat. Grasses in some alpine meadows may be unable to find patches of appropriate soil at higher elevations, while the insect and mammal herbivores that feed on those grasses may be able to move to mountains with higher meadows. Paleoecologists have described just such individualistic responses to past major climate changes. Many communities existed in the past but do not occur today (Davis and Zabinski 1992). These “non-analog” communities may have been the result of different response times of component species to a changing climate, or may have been the result of non-analog climates (Pielou 1992).

Thus, an alternative prediction to simple ecosystem movement is that the denizens of diverse ecosystems and communities will have divergent responses to climate shifts. The net effect of these responses may be the eventual creation of new community types as species abundances change, new species invade, and some species go extinct. With current climate change, some existing ecosystems may disappear and new ones may arise in their stead. Unfortunately, the complexity of these effects makes them very difficult to anticipate or model with any precision.

### *Responses to extreme weather*

What *is* clear from basic ecological and physiological research is that natural systems are strongly influenced by extremes of weather and climate (reviewed by Parmesan et al. 2000 and Easterling et al. 2000 a,b). One of the very

first such studies dates back to the nineteenth century when Bumpus (1899) documented that a severe winter storm over Lake Michigan disproportionately killed off both the largest and the smallest sparrows, thereby generating strong natural selection on body size.

Many biological processes undergo sudden shifts at particular thresholds for temperature or precipitation (Precht et al. 1973; Weiser 1973; Hoffman and Parsons 1997). Tolerances to frost and to low levels of precipitation often determine plant and animal range boundaries (Andrewartha and Birch 1954; Woodward 1987). For example, trees only occur where annual precipitation is above 300 mm. Further, tropical trees are killed by low temperatures ranging from 0°C to 10°C, whereas temperate broad-leaved deciduous trees can survive temperatures to -40°C, and many boreal species appear to be able to survive any extreme low (Woodward 1987). An extended drought in New Mexico in the 1950s caused the boundary between pine and pinyon-juniper forest to shift by 2 km, where it remains today (Allen and Breshears 1998). Animals exhibit similar climate restrictions. For instance, the nine-banded armadillo (*Dasypus novemcinctus*) requires more than 38 cm annual precipitation and is further restricted to latitudes with fewer than 20–24 days below freezing throughout winter and to fewer than nine consecutive days below freezing (Taulman and Robbins 1996).

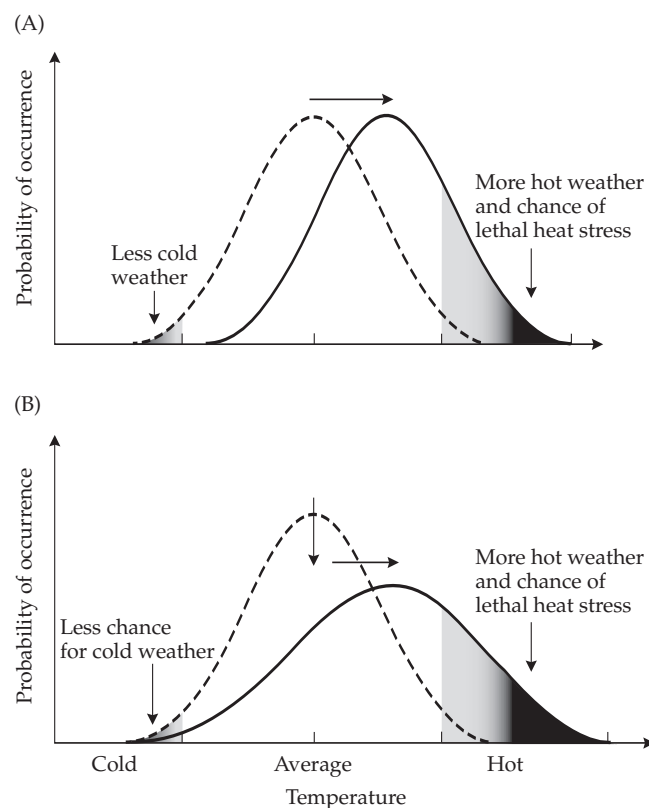
Single extreme temperature and precipitation events can have profound and long-lasting effects on physical characteristics. Drought years in the Galápagos, induced by El Niño, cause evolution of larger beak size in Darwin's Finches (*Geospiza fortis*), while extremely wet years drive evolution of small beak (and body) size (Boag and Grant 1984). Perhaps the most extreme example is that in many reptiles, an individual's sex is determined by the maximum temperature experienced during a critical phase of embryonic development (Bull 1980; Janzen 1994). Experiments with map turtles (*Graptemys* spp.) showed that maximum incubation temperatures below 28°C produce only males, whereas maximum temperatures surpassing 30°C produce only females (Bull and Vogt 1979). Even under the current climate, single-sex nests are common. Thus even small changes in temperature extremes could result in single-sex populations, with obvious conservation implications.

Insect species are well known for their boom and bust cycles, with much of that variation having been linked to climate. Single drought years have been shown to affect individual fitness and population dynamics of many insects, causing drastic crashes in some species (Singer and Ehrlich 1979; Ehrlich et al. 1980; Hawkins and Holyoak 1998), while leading to population booms in others (Mattson and Haack 1987).

Many studies have related El Niño events to changes in marine biotic systems (Roemmich and McGowan

1995; Sagarin et al. 1999). Particularly striking were widespread massive coral bleaching events that followed the 1982–1983 and the 1997–1998 intense El Niños (Coffroth et al. 1990; Glynn 1990; Hoegh-Guldberg 1999). Host–parasite interactions including infectious diseases are influenced by climatic factors (such as El Niño) in terrestrial and marine communities, and these links are likely to be altered with a changing climate (Harvell et al. 2002). Finally, ecosystem structure and function are affected by disturbance events, many of which are associated with tornadoes, floods, and tropical storms (Pickett and White 1985; Walker and Willig 1999).

In summary, even if the statistical distribution of extreme events remains the same, the absolute number of days that lie outside of the physiological tolerance of a particular species may increase (Figure 10.10; Schärri et al. 2004). Further, this increase in extremes is most likely



**Figure 10.10** Increases in mean temperature and temperature variability will affect the probability that an individual experiences extreme events. Areas in gray represent temperatures at which an individual suffers heat stress or cold stress; areas in black represent lethal hot or cold temperatures. (A) An increase in mean temperature, leading to more record hot weather, will lead to greater heat stress and lethal heat events, and less cold stress. (B) An increase in both the mean temperature and variance, leading to much greater heat stress and lethal hot weather events, and less cold stress. (Modified from IPCC 2001c.)

to affect populations and individuals at the edge of the species range where individuals are often living at the limit of their species' physiological tolerances and thus are susceptible to stressful, harmful, or lethal weather events (Hoffman and Parsons 1997). The predicted increases in extreme temperature and precipitation events are expected to lead to physical and behavioral changes in a few species, to dramatic changes in the distributions of many species, and to population and even species extinction in the worst cases (Parmesan et al. 2000).

## Observed Biological Impacts of Climate Change

Twentieth century warming was but a fraction of what flora and fauna dealt with during the last glacial–interglacial cycle. In contrast, however, humans have had enormous negative impacts on biodiversity through massive habitat destruction and fragmentation, loading of natural systems with nutrients and toxins from cars and industry, widespread overexploitation of populations, and the introduction of nonnative species over the past century. Increasingly we are observing changes in wild systems that have been linked to climatic trends. Though most effects have been relatively minor and benign, it is clear that the continuation of observed trends is likely to have profound impacts on wild species and consequently on the ways in which the conservation community strives to preserve biodiversity.

### *Detection and attribution*

Given the many ways humans have been altering species' distributions and influencing local population abundances for thousands of years, and most strongly over the past 100 years, how is it possible to detect an influence of climate change on wildlife? Given that a response is detected, what is its relative impact with respect to other anthropogenic stressors? If the impacts of climate change are relatively weak and buried within a general framework of human-mediated habitat deterioration, is climate change, in itself, important? Addressing these questions in a scientifically rigorous manner is difficult, but is essential for determining the conservation implications of climate change.

The first question has been addressed in several recent reviews and analyses, which show that twentieth century climate change has had a wide range of consequences and has impacted many diverse taxa in disparate geographic regions (Easterling et al. 2000b; Hughes 2000; IPCC 2001b; Peñuelas and Filella 2001; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). However, this seemingly simple statement glosses over the enormous difficulties biologists have had in tackling

the question of climate change impacts. A basic problem is that studies used to assess climate change impacts are, of necessity, correlational rather than experimental. Therefore, interpretation of biological changes requires less direct, more inferential methods of scientific inquiry (e.g., Sagarin and Micheli 2001). Further, detecting significant trends in long-term datasets is particularly difficult when data are often patchy in quantity and quality, and when natural yearly fluctuations are typically noisy. Once change has been detected, attributing the cause of the biological change to climate change requires consideration of multiple nonclimatic factors that may confound effects of climate.

It is no surprise, then, that *detection* and *attribution* are prime issues for scientific assessment teams such as the IPCC. The search for such a climate "signal" in natural systems has been a challenge for climate change biologists. Some studies have attempted to conduct research that filters out effects of confounding forces, such as habitat degradation, by utilizing data from relatively pristine areas. Even so, detecting long-term trends in say, population abundances, has been difficult unless the data have been consistently collected over several decades and at regional or continental scales.

Using various methods to deal with these difficulties, responses to climate change have been detected in individual studies conducted from the population to the community level, as well as on ecosystem processes. The following is a selection of such studies that exemplify the links between biotic changes and climate change since the mid-1800s.

### *Evolutionary and morphological changes*

A factor often downplayed in discussions of responses to global warming is the propensity for evolution of a population in situ to the selective forces brought about by climate change. A single unambiguous study in the U.S. documented rapid evolution of an introduced species to fit a gradient of climate conditions in the region where it was introduced (Huey et al. 2000). In its native Europe, the fly *Drosophila subobscura* has longer wings in northern countries than in southern countries. Just after being introduced to the western U.S., the flies all had the same wing length. Twenty years later, however, the flies had mimicked their European ancestors by evolving to fit the temperature gradient from south to north: wing lengths became shorter in southern California, gradually increasing in length north to Oregon. This demonstrates that wild species can respond rapidly to local climate conditions.

However, introduced species probably comprise a somewhat artificial situation and this result may tell us little about observed or potential evolutionary responses of native U.S. species to climate change. A major eco-

logical theory postulates that the tremendous success of some invasive species can be attributed to their release from predators or coevolved parasites, diseases, and pathogens (Williamson 1996; Keane and Crawley 2002), which sufficiently decrease selective pressures to allow the organism to lose many of its adaptations for deterring or coping with enemy attack. Maintenance of defense mechanisms is thought to constrain an organism in other ways. For instance, the cost of defense might result in reduced growth or reproduction, or an inability to respond to selection for coping with climatic extremes. Freedom from the need for defense might allow the evolution of novel traits, such as those associated with climate adaptation. Thus, invasive species might be better able to evolve adaptations to cope with a changing climate than native species, which operate under more adaptive constraints.

It is inherently difficult to address the question of how common it is for a population to respond to climate change through genetic evolution. Very few studies have documented an evolutionary response, but there are few systems in which there is the potential for such documentation because the question requires historical data on frequencies of genetically based traits to compare with modern frequencies. It's not surprising, then, that several of the handful of such studies are on the model genetic system—fruit flies in the genus *Drosophila*.

Geneticists in the 1950s noticed that certain types of chromosomal inversions were associated with heat tolerance. These "hot" genotypes were seen to increase in frequency during a season, as temperatures rose from early spring through late summer, and to increase in frequency in southern populations as compared to northern. Increases in frequencies of warm-adapted genotypes and decreases in cold-adapted genotypes have been observed in wild populations of *D. subobscura* fruit flies in Spain between studies conducted in 1976 compared to 1991 (Rodríguez-Trelles et al. 1996; Rodríguez-Trelles and Rodríguez 1998; Rodríguez-Trelles et al. 1998). An analogous study on *D. robusta* in the northeast U.S. that used genetic data going back to 1946 also found increases in warm genotypes and decreases in "cool" genotypes in all populations sampled (Levitan 2003). This change was so great that populations in New York in 2002 were converging on genotype frequencies found in Missouri in 1946.

A study in Britain indicated evolution at the northern range edge of a grasshopper toward a greater frequency of long-winged individuals, which have better dispersal capabilities (Thomas et al. 2001). Thus, this grasshopper was able to colonize northward faster than was expected from average dispersal abilities within old populations. This is an intriguing finding, in that it suggests that species may be able to shift their ranges relatively quickly in response to changing climate.

Studies of small mammals in the southwestern U.S. have provided excellent documentation of physical changes in response to both historical and current climate change. Small mammals have exhibited relatively slight range shifts since the last glacial maximum compared to insects and plants. This might give the impression that these animals are little affected by climatic regime. Quite the contrary is evident from both paleoecological studies and modern studies. A study in New Mexico on white-throated wood rats (*Neotoma albigula*) showed that these small mammals responded to warmer winters and hotter summers over eight years (1989–1998) by getting 16% smaller (Smith and Betancourt 1998). This study was able to pinpoint the 2–3°C rise in temperature as the driver of the size change, showing that changes in precipitation were not correlated with size changes. However, the detailed reasons for this response are still unknown. For instance, it is not known whether the size changes are *plastic* (i.e., changes within an individual within its lifetime) or *genetic* (i.e., changes in genotypes from one generation to the next). Neither is it known *why* size changes with temperature. Being smaller may reduce overheating in the summer, warmer winters may increase survival of the smallest individuals, or size may reflect a response to changes in food availability.

A conservation application suggested by these studies might be the deliberate transfer of southern individuals into more northerly populations in the hopes of facilitating local evolutionary response to rapid climate warming. This might be particularly important for populations of endangered species that are geographically isolated from other populations and unlikely to receive natural gene flow from populations that carry other climate-adapted genotypes. However, such translocation will change the evolutionary trajectories of such populations by altering their genetic composition, which could have negative consequences, and could alter the nature of interactions of the target species with other community members, and for these reasons, conservationists are also wary of such steps. Certainly, the potential benefits and dangers of interventions to help species cope with climate change will need to be considered carefully.

### **Phenological shifts**

Humans have long been interested in the events marking the beginning of spring, such as blooming of the first spring flower, leafing out of popular trees, and nest-building by birds. The timing, or phenology, of these events is commonly caused by seasonal temperature changes (e.g., the number of days above a certain °C), photoperiod (the amount of daylight, which varies predictably over the course of a year), lunar tides, seasonal weather (e.g., floods or monsoons), and the phenologies of other organisms (e.g., the arrival of a migratory prey

species). Phenologies can often be very precise in their timing and coordination, as with the breeding of corals or the hatching of sea turtles. Not all of these events would be affected by climate changes, of course. But many species' phenologies are driven directly or indirectly by temperature cues.

Studies in North America and Europe provide strong evidence that global climate change has already caused changes in the timing of biological events. Brown et al. (1999) studied Mexican Jays, *Aphelocoma ultramarina*, in the Chiricahua Mountains of southern Arizona and showed that between 1971 and 1998 the breeding season of the study birds advanced by 10 days on average. The laying date of first clutches was significantly correlated with April monthly minimum temperatures, which increased by about 2.5°C. Dunn and Winkler (1999) used more than 3400 nest records on the timing of the initiation of breeding in Tree Swallows, *Tachycineta bicolor*, throughout their range in the contiguous 48 states and Canada. During 24 years with adequate data (1959–1991), the authors were able to show that the timing of laying was significantly correlated with the mean May temperature and that the average date of laying advanced by 9 days.

Bradley and colleagues (1999) were able to take advantage of observations made by Aldo Leopold at a Wisconsin farm in the 1930s and 1940s on the timing of spring events for birds and native flowers. Comparing these data to their own surveys in the 1980s and 1990s enabled them to look for long-term trends over the 61-year period. For example, Northern Cardinals (*Cardinalis cardinalis*) were heard singing 22 days earlier, and butterfly milkweed (*Asclepias tuberosa*) was blooming 18 days earlier. Of 55 species studied, 19 (35%) showed advancement of spring events. On average, spring events occurred 7.6 days earlier by the 1990s compared to 61 years before, coinciding with March temperatures being 2.8°C warmer.

One other long-term (100-year) study focused on frogs in Ithaca, New York. Gibbs and Breisch (2001) compared recent records (1990–1999) with a turn of the century study (1900–1912). They found that in four of six species, males begin courtship calling 10–13 days earlier than they did in the early 1900s (the other two species showed no change). Maximum temperature in the study area has increased 1.0°C–2.3°C during five of the eight months critical for the frog reproductive cycle. Other studies of frogs have shown that reproduction is closely linked to both nighttime and daytime temperatures (Beebee 1995).

In the U.K. Crick et al. (1997), analyzing more than 74,000 nest records from 65 bird species between 1971 and 1995, found that the mean laying dates of first clutches for 20 species had advanced by, on average, 8.8 days, similar to the 10 and 9 days found in the U.S. studies. Butterflies in Europe show similar correlations of dates of first appearance and spring temperatures, as

well as a recent advancement of first appearance in 26 of 35 species total (Roy and Sparks 2000). In Great Britain, the red admiral (*Vanessa atalanta*) is appearing more than a month earlier than it did 20 years ago. Amphibian breeding has advanced by 1–3 weeks per decade in England (Beebee 1995). Throughout Europe, trees are leafing out earlier, shrubs and herbs are flowering earlier, and fall colors are coming later, leading to an overall lengthening of the vegetative growing season by nearly 11 days since 1960 (Menzel and Fabian 1999; Menzel 2000).

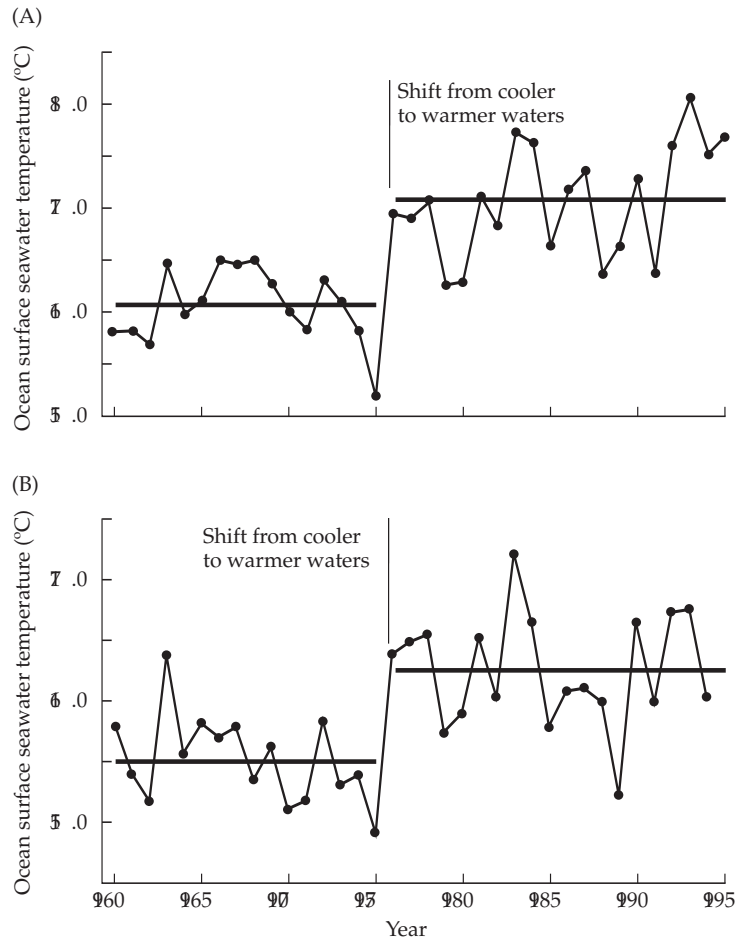
Some species may also experience phenology conflict, which can occur when breeding or growth events have different clock references. In one European bird species—the Pied Flycatcher (*Ficedula hypoleuca*)—egg-laying is determined by photoperiod but the departure for southern migration is set by temperature, squeezing just-hatched chicks between both events and forcing them to develop quickly enough to be able to fly long-distances effectively (Both and Visser 2001).

### **Abundance changes and community reassembly**

For many species, climate has been shown to have a direct impact on population size. Sillett et al. (2000) studied the Black-throated Blue Warbler (*Dendroica caerulescens*), a species that migrates between temperate North America (the breeding range) and Central America and the Caribbean (the overwintering range). Over a ten-year period the authors tracked a correlation between population dynamics and El Niño-La Niña years. The cycle, known as the El Niño Southern Oscillation (ENSO), is a powerful but predictable weather pattern that influences precipitation and temperature during a multimonth period over much of the Western Hemisphere. El Niño years tended to reduce available food during winter; La Niña years had abundant food and much higher survival rates for overwintering birds. Fecundity and survivorship of hatchlings of birds in the breeding range was also influenced, with much lower fledgling mass during El Niño years relative to La Niña years. Again, this variance was associated with changes in food abundance based on rainfall levels. The study implies that long-distance migrants and species that depend on large-scale dispersal might be just as at risk of negative climate effects as are sedentary species.

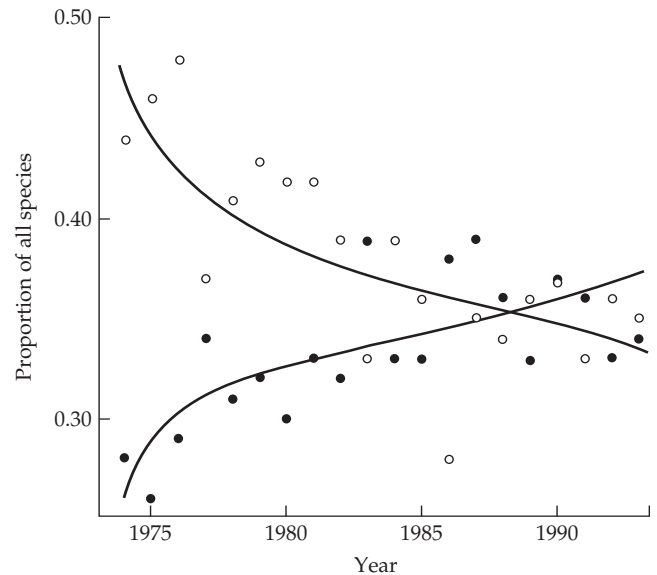
Changes in the structure of local plant and animal communities indicate that at some study sites the more warm-adapted species are flourishing while more cold-adapted species are declining. This has been particularly well-documented in the Californian coastal waters of the Pacific, which have experienced a 60-year period of significant warming in nearshore sea temperatures (Figure 10.11; Barry et al. 1995; Holbrook et al. 1997; Sagarin et al. 1999).

A marine sanctuary in Monterey Bay has provided a valuable, relatively undisturbed environment to look for responses to this rise in ocean temperatures. In addition,



**Figure 10.11** Mean annual ocean surface temperatures at (A) Scripps Pier and (B) Santa Barbara, California, from 1960 to 1995. Horizontal lines indicate long-term mean temperatures for the periods of 1960–1975 and 1976–1995. Leaders indicate a regime shift from cooler to warmer waters during 1976–1977. (Modified from Holbrook et al. 1997.)

Monterey Bay is an interesting example because it is located in a small region of overlap between northern species (that extend their ranges all the way to Alaska), and southern species (whose ranges extend down to Mexico). Fixed plots were established in 1931, which researchers in the 1990s were able to locate and resurvey. They found that, compared to the earlier survey, abundances of nearly all southern species had increased significantly while abundances of nearly all northern species decreased (Barry et al. 1995; Sagarin et al. 1999). Thus the dominance relationships in this intertidal community have shifted markedly in response to water temperature change. Holbrook et al. (1997) found similar shifts over the past 25 years in kelp forest fish communities off southern California (Figure 10.12). Southern species have greatly increased their proportionate dominance of community composition at the expense of more northern species. Farther offshore, Roemmich and McGowan (1995) showed that over 43 years (1951–1993) of this temperature change, the population abundance of plankton species also was reduced greatly. Taken as a whole, this body of work in the California Current and associated intertidal areas has demonstrated clear effects of warming sea temperatures on vertebrate and invertebrate communities.



**Figure 10.12** Proportions of the species of kelp forest fish present that were northern (open circles) or southern (closed circles) during censuses off of southern California from 1974 to 1995. (Modified from Holbrook et al. 1997.)

Some plant communities in North America have shown increase in woody species relative to grasses and herbs. In experimental manipulations, multiple individual factors, (increased temperature, increased water availability, and increased CO<sub>2</sub>) have all resulted in increases in woody species in plant communities (Harte and Shaw 1995; Chapin et al. 1995). Large-scale trends in this direction appear to be occurring in diverse landscapes, from Alaskan tundra (Chapin et al. 1995; Sturm et al. 2001) to the desert Southwest (Turner 1990; McPherson and Wright 1990; Brown et al. 1997). Though overgrazing is partially responsible in given locales, experimental results suggest that the general phenomenon also stems from the joint effects of increases in all three of these factors (temperature, water, carbon dioxide) in these regions (Archer 1995).

### Range shifts

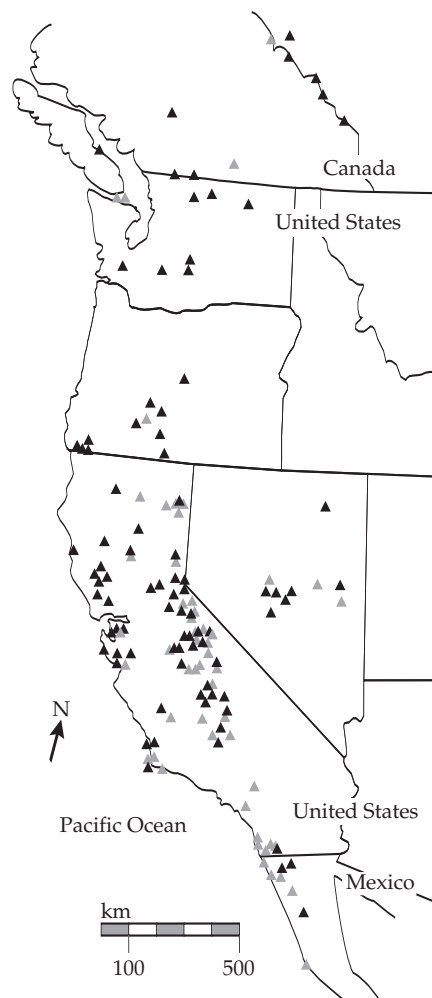
Range shifts are changes in the geographic distribution of a species. By analyzing preserved remains of plants, insects, mammals, and other organisms that were deposited during the most recent glacial and interglacial cycles, scientists have been able to track where different species lived at times when global temperatures were either much warmer or much cooler than today's climate. The range of most species was several hundred km closer to the equator or several hundred meters lower in elevation during times when Earth was in a glacial period—that is, 4°C–5°C cooler than it is today (Cox and Moore 2000).

A study of the 59 breeding bird species in Great Britain showed both expansions and contractions of the different northern range boundaries, but northward movements were of a greater magnitude than southward movements, with a mean northward shift of 18.9 km over a 20-year period (Thomas and Lennon 1999). For a few well-documented species, it has been shown that the northern U.K. boundaries have tracked winter temperatures for over 130 years (Williamson 1975). Further, higher reproductive success has been linked to warmer springtime temperatures (Visser et al. 1998). Physiological studies indicate that the northern boundaries of North American songbirds may generally be limited by winter nighttime temperatures (Root 1988a,b).

In Canada, the red fox (*Vulpes vulpes*) has expanded northward over the past 70 years while the arctic fox (*Alopex lagopus*) has contracted toward the Arctic Ocean (Hersteinsson and MacDonald 1992). The timings of the boundary changes have tracked warming phases. Occasional accidental transplants of the arctic fox southward from its range limit had succeeded, provided that the red fox, which is competitively dominant was locally absent. However, prior to recent climatic warming, multiple accidental transplants of the red fox north of its range limit had failed. The red fox has physical attributes that make it less adapted to cold conditions than the arctic fox (e.g., longer ears and limbs). From this it has been inferred

that the expansion of the red fox is due to warming trends, causing the competitively inferior arctic fox to retreat northward.

On a continental scale, movements of entire species' ranges have been found in butterflies in both North America and Europe, where two-thirds of the 58 species studied have shifted their ranges northward by as much as 100 km per decade (Parmesan 1996; Parmesan et al. 1999). The first study to document such a species-wide range shift was with Edith's checkerspot butterfly (*Euphydryas editha*). Population extinctions were four times higher along the southern range boundary (in Baja, Mexico) than along the northern range boundary (in Canada), and nearly three times higher at lower elevations (below 8000 feet) than at higher elevations (from 8000 to 12,500 feet) (Figure 10.13; Parmesan 1996). In concert with glob-



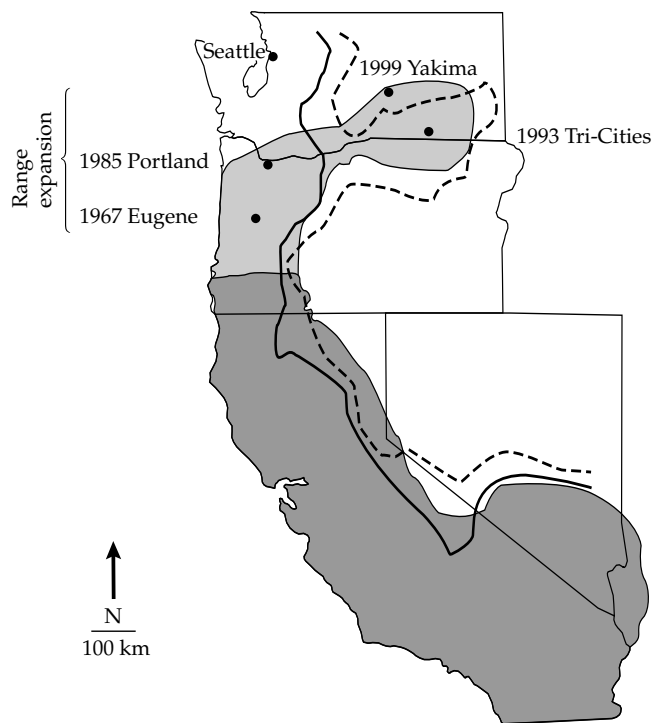
**Figure 10.13** Patterns of population extinctions of *Euphydryas editha* from 1860 to 1996. Each triangle represents a single population. Historical records are from 1860 to 1983. Black represents populations still present during the 1994–1996 census. Gray represents populations recorded as extinct during the 1994–1996 census. (From Parmesan 1996.)

al warming predictions, this extinction process had effectively shifted the range of *E. editha* northward 92 km, and upward 124 m in elevation since the beginning of the century (Parmesan 1996). This closely matched the observed warming trend over the same region, in which the mean yearly temperature isotherms had shifted 105 km northward and 105 km upward (Karl et al. 1996). No other factor could explain the observed range shift.

Butterflies have, in fact, provided some of the best studies of climate constraints and climate change impacts. Seventy years of published studies document the limiting effects of temperature on butterfly population dynamics, particularly at northern range edges (Pollard 1988; Dennis 1993; Parmesan 2003). The northern boundaries of many European butterflies are correlated with summertime temperature isotherms, and recent expansion matches predictions from models based solely on temperature constraints (Thomas 1993; Warren et al. 2001). Populations toward the northern boundary become increasingly confined to the warmest microclimates (e.g., short turf and south-facing hills) (Thomas 1993; Warren et al. 2001). Transplants beyond the northern boundary have failed to sustain breeding colonies, even when the habitat appeared suitable (Ford 1945).

The sachem skipper butterfly (*Atalopedes campestris*) has expanded from California to Washington State (420 miles) in just 35 years (Crozier 2003a,b; Figure 10.14). During a single year—the warmest on record (1998)—it moved 75 miles northward. Laboratory and field manipulations showed that individuals are killed by a single, short exposure to extreme low temperatures ( $-10^{\circ}\text{C}$ ), or repeated exposures to  $-4^{\circ}\text{C}$ , indicating that the northern range limit is dictated by winter cold extremes (Crozier 2003a). As climate continues to reduce the number and severity of winter extreme cold events, the northward spread of this species, as well as others with similar limitations, should continue.

Montane studies have generally been more scarce, but the few that exist show a general movement of species upward in elevation. Lowland birds have begun breeding on mountain slopes in Costa Rica (Pounds et al. 1999; see Case Study 10.2 by Karen Masters, Alan Pounds, and Michael Fogdon), alpine flora have expanded toward the summits in Switzerland (Grabherr et al. 1994), and Edith's checkerspot butterfly has shifted upward by 105 m in the Sierra Nevada of California (Parmesan 1996). Globally, several studies show poleward and upward movement of treeline in certain locales (Kullman 2001; Moiseev and Shiyatov 2003). Within North America, general upward movement of treeline has occurred in the Canadian Rockies as temperatures rose by  $1.5^{\circ}\text{C}$  (Luckman and Kavanagh 2000). However, the precise locations of treelines result from a complex response to temperature, precipitation, fire regimes, and outbreaks of pathogens and herbivores. This whole complex of factors determines the local elevations and lati-



**Figure 10.14** The overwintering range of the sachem skipper butterfly (*Atalopedes campestris*) includes Washington, Oregon, California, and Nevada. The historical range is shaded dark, while range expansion over the past three decades is shown in lighter shading. Colonization dates of *A. campestris* in four cities in Oregon and Washington are shown. Contour lines represent the boundary of January average minimum temperature of  $0^{\circ}\text{C}$  (solid) and  $-4^{\circ}\text{C}$  (dashed). (From Crozier 2003b.)

tudes of treeline (Luckman and Kavanagh 2000; Grace et al. 2002). Further, mechanistically, patterns of variability in temperature and precipitation are considered to be far more important than simple averages (Swetnam and Betsanourt 1998).

### Sea level rise

Sea level rise has caused some contractions in the distributions of coastal species. The pine forest barrens in the Florida Keys have been steadily pushed out of the lowest-lying areas because of increased ground water salinity caused by sea level rise (Ross et al. 1994). They are now restricted to the hillier areas, which has resulted in habitat loss for species that depend on the pine barrens.

Since the 1940s, one of the salt marshes of Barn Island, Rhode Island, has undergone large changes in vegetation community composition, with increases in cover of low marsh species such as *Spartina alterniflora*, forbs, and graminoids, at the expense of the high marsh communities (dominated by *S. patens* and *Juncus gerardii*) (Warren and Niering 1993). At Barn Island, response to rising sea

level is not a simple landward shift of individual species, but a shift in the entire marsh community toward low marsh species. Warren and Niering suggested that sea level rise has been faster than the rate of new accumulation of appropriate marsh substrate, leading to less habitat for high marsh species. Sam Pearsall of The Nature Conservancy discusses potential mitigation measures to cope with sea level rise in eastern North Carolina in Case Study 10.3.

### **Direct effects of carbon dioxide**

Some greenhouse gases may have biotic effects in themselves. The carbon from atmospheric CO<sub>2</sub> is essential for plants in many ways: Carbon is used to make sugars and starch, is a fundamental component of secondary compounds (e.g., defensive agents against being eaten or attacked by disease), and is the building block of plant structures. If the amount of carbon available to the plant increases, such as through increased atmospheric CO<sub>2</sub> concentrations, then the types and quantities of carbon-containing compounds also change (Peñuelas and Estiarte 1998). For these reasons, increased atmospheric carbon dioxide has been shown to act as a plant “fertilizer.” In experiments that increase concentrations of CO<sub>2</sub>, plants respond with increased growth. A review of experimental studies found that atmospheric concentrations of 650 ppm stimulated photosynthesis by 60%, the growth of young trees by 73%, and wood growth per unit of leaf area by 27% (Keeling and Whorf 1999).

Another major effect is that increasing atmospheric CO<sub>2</sub> has been shown to increase the carbon–nitrogen (C:N) ratio in plants (reviewed by Cotrufo et al. 1998; Bezemer and Jones 1998). Insects that feed on plant tissues are very sensitive to the C:N ratio, and may alter their diet preferences, growth rates and fecundity in response to changes in this ratio. Bezemer and Jones (1998) reviewed experimental studies that compared insect performance when fed host plants grown at ambient CO<sub>2</sub> levels (around 350 ppm) versus plants grown at high CO<sub>2</sub> levels (650–700 ppm). The study used data published for 43 insect species (from aphids to beetles to flies) and 42 plant species (from small herbs to trees). As expected, percent nitrogen was lower and carbon-containing compounds were higher (storage, structure, and defensive compounds) for plants raised in high CO<sub>2</sub>. The surprising finding was how idiosyncratic insect responses were to the changes in their host plants. Leaf chewers (such as the lepidoptera, butterflies and moths) tended to eat more, take longer to develop, be smaller, and were more likely to die when fed high CO<sub>2</sub> host plants. This is expected because nitrogen is a limiting factor for their development and hence they do worse on the high CO<sub>2</sub>/low nitrogen plants, resulting in much lower population sizes. The high CO<sub>2</sub> plants also had

much higher concentrations of phenolics and terpenes—secondary compounds that act as a defense against lepidoptera. What is more surprising is that other insect groups, such as the phloem feeders (including aphids), actually had *faster* developmental time and attained *higher* population numbers on high CO<sub>2</sub> plants.

Alteration in the amount or timing of floral resources are likely to have large influences on the fitness of nectaring adults, such as bees, wasps, butterflies, and moths. This would be particularly true for insects that are tightly coevolved with a specific plant species. In a study by Rusterholz and Erhardt (1998), doubled CO<sub>2</sub> levels had dramatic effects on floral resources commonly used by butterflies in Switzerland. They exposed five species of common flowering herbs and shrubs to ambient or doubled CO<sub>2</sub>. For those species that showed a significant response, high CO<sub>2</sub> led to earlier flowering and more flowers being produced. High CO<sub>2</sub> flowers also contained significantly less nectar, generally higher sugar concentrations, lower total amino acids, and altered amino acid compositions. Butterflies have strong species-specific preferences for nectar quantity and composition. The concern for conservation is that recovery by endangered butterfly species may be affected by these subtle changes in floral resources in the wild.

### **Ecosystem process changes**

Are we seeing changes in the flows of energy and nutrients in the biosphere? This process is often referred to as “ecosystem functioning,” and is difficult to assess even in the absence of environmental change. Rather than tackle that question directly, it is easier to detect changes in specific components of ecosystem flows and processes. As discussed earlier the length of the growing season is increasing (Myneni et al. 1997; Zhou et al. 2001; Lucht et al. 2002). Because plants are a major intermediary for carbon flow through ecosystems, this lengthening of the active period has altered the annual cycle of carbon dioxide levels in the atmosphere (Keeling et al. 1996).

The Alaskan tundra has historically been a CO<sub>2</sub> sink, but that may be changing. Historically, when tundra plants die, they quickly become part of a frozen layer of organic matter. Even in midsummer, only the very upper surface of this layer defrosts. When this dead matter is frozen, it is in storage. The soil organisms that break it down are able to function only if it gets above freezing, and the warmer it is, the faster they work. The Alaskan tundra has already experienced much stronger warming trends than the rest of the U.S. At some point, as deeper layers remain above freezing, the rate of decomposition of dead matter will exceed the rate of plant growth, and the tundra will turn from a net sink to a net source of CO<sub>2</sub>.

This switch from net sink to net source is already occurring in some tundra areas. Oechel et al. (1993) found

that at Toolik Lake and Prudhoe Bay, Alaska, during 1983–1987 and 1990, the tundra was acting as a source of CO<sub>2</sub> to the atmosphere. This was associated with long-term atmospheric and soil temperature increases, soil drying, and increased depth to water table. By 1998, moderate acclimation resulted in a return to the tundra acting as a sink in summer (Oechel et al. 2000). However, warmer winters continue to cause an overall net loss of carbon.

Lengthening of the growing season is expected to generally increase carbon uptake simply by allowing more time for biomass accumulation. Indeed, net primary productivity (NPP) has increased both across North America (Hicke et al. 2002) and globally (Nemani et al. 2003). However, recent increased carbon storage in the eastern U.S. stems largely from regrowth of trees on previously logged mature forest and abandoned agricultural land and not from regional climate change (Fan et al. 1998; Schimel et al. 2000). In contrast, the switch across boreal forests to becoming carbon sources is believed to stem directly and indirectly from regional climate change. The warming and drying trends in the boreal regions of North America have been linked to reduced tree growth due to water stress (Barber et al. 2000), increased pest outbreaks, and increased incidences of wildfire (Kurz and Apps 1999).

These trends are not likely to be stable, as the underlying processes are dynamic and, to some extent, unpredictable. Once the regrowth occurring in the eastern U.S. becomes mature forest, the rate of carbon uptake will be substantially reduced. Likewise, fertilization effects of increased CO<sub>2</sub> and nitrogen are short term, having a positive effect only until some other resource becomes limiting to plant growth. As discussed earlier, climate changes are causing major shifts in community structure, and different vegetation communities have very different carbon cycling and storage properties (open tundra differs from spruce forest, for example). Therefore, current patterns of carbon uptake and emission from terrestrial vegetation are likely to change considerably over the next few decades.

### ***The global picture: A synthesis of biological impacts***

Several recent reviews and global analyses across individual studies provide convincing evidence that twentieth century climate change has already affected Earth's biota (Hughes 2000; IPCC 2001b; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). This conclusion is particularly compelling because the patterns of biological change are similar regardless of the taxonomic group or geographic region.

However, a skeptic might be wary of extrapolating from those individual studies to global biodiversity im-

pacts. The publication process has been accused of “cherry picking” studies that show an impact. This effect is known as a “positive publishing bias,” and stems from a fundamental human trait to be more interested in reporting that something is happening than not. Consider a researcher returning to the same site every year and recording that numbers of “wattling widgets” is exactly the same now as it was 30 years ago. This type of information might go into a yearly field station report, but is unlikely to become accessible to the scientific community at large through publication in peer-reviewed literature.

A meta-study by Parmesan and Yohe (2003) sought to address this problem. This synthesis focused on multi-species studies; hence, species that have not responded to recent climate change were documented along with those exhibiting responses, allowing for an estimate of overall impact of climate change to be made. In all, this study combined data from more than 1700 species across the globe. Interestingly, the skeptics were partly right—about half of the species in this study were stable, showing no response.

On the other hand, the changes that were observed were not random, but were systematically in the direction expected from regional changes in climate. Over the past 20–140 years, an alarming 50% of all species studied exhibited significant responses to regional warming trends by showing earlier phenology (timing of breeding or emerging events), a shift in their distributions toward the poles and higher elevations, or both. These responses have been occurring in diverse ecosystems (from temperate terrestrial grasslands to marine intertidal communities to tropical cloud forest), and in many types of organisms (e.g., birds, butterflies, sea urchins, trees, and mountain flowers) (Table 10.1; Parmesan and Yohe 2003).

Important diagnostic patterns, specific to climate change impacts, helped provide a “fingerprint” of global climate change as the driver of the observed changes in natural systems. Species with more than 70 years of annual data showed signs of tracking decadal temperature swings, such as shifting southward during cool periods and northward during warm periods. At sites where northern and southern communities overlap, the northerly (cold-adapted) species declined while the southerly (warm-adapted) species increased. Such diagnostic “sign-switching” responses were observed in 294 species, spread across the globe and ranging from oceanic fish to tropical birds to European butterflies (Parmesan and Yohe 2003).

One of the most important aspects of warming trends may occur at the community level. Climate change appears to affect each species differently (hence the variation in response in Parmesan and Yohe's [2003]; see Table 10.1). Thus, individualistic changes in distribution, abundance, and phenology are likely to alter interspecies

**TABLE 10.1** A Summary of Observed Changes from Studies of 944 Species

Climate change prediction	Changed as predicted (%)	Changed opposite to prediction (%)	Statistical likelihood of obtaining pattern by chance
Earlier timing of spring events	87	13	Very unlikely
Extensions of poleward or upper species' range boundaries	81	19	Very unlikely
Community (abundance) predictions: Cold-adapted species declining and warm-adapted species increasing	85	15	Very unlikely

Source: Data from Parmesan and Yohe 2003.

relationships such as competition, predation, and parasitism. Particular effects will be very difficult to predict, but community reassembly (potentially disassembly) and disruptions of species interactions could prove to be the most widespread and worrisome biotic impacts of climate change (see Case Study 10.1).

## Conservation Implications of Climate Change

Earth's ecosystems face a scale of climate-related change that has not been seen for many thousands of years and that will continue for centuries. The best available climate models suggest that most of Earth's terrestrial zones and all of its aquatic systems will be altered as a result. Many studies also suggest that some impacts can already be seen. The logical extrapolation from these observed impacts is that there will be large changes in communities and increased numbers of species' extinctions.

### Extinctions

Extinctions have been occurring at a higher rate in recent centuries for a variety of anthropogenic causes, but climate change is likely to exacerbate population declines sufficiently for some species to completely disappear. To date, there have been only two extinctions directly attributable to climate change, the golden toad and harlequin frog in Costa Rica (see Case Study 10.2). Conservation biologists, however, are also concerned with the loss of a distinct subspecies or with loss of all individuals of one species in a given geographic area (e.g., cougars in the southern U.S. Rocky Mountains). Drastic regional declines of this type have already been directly attributed to climate change.

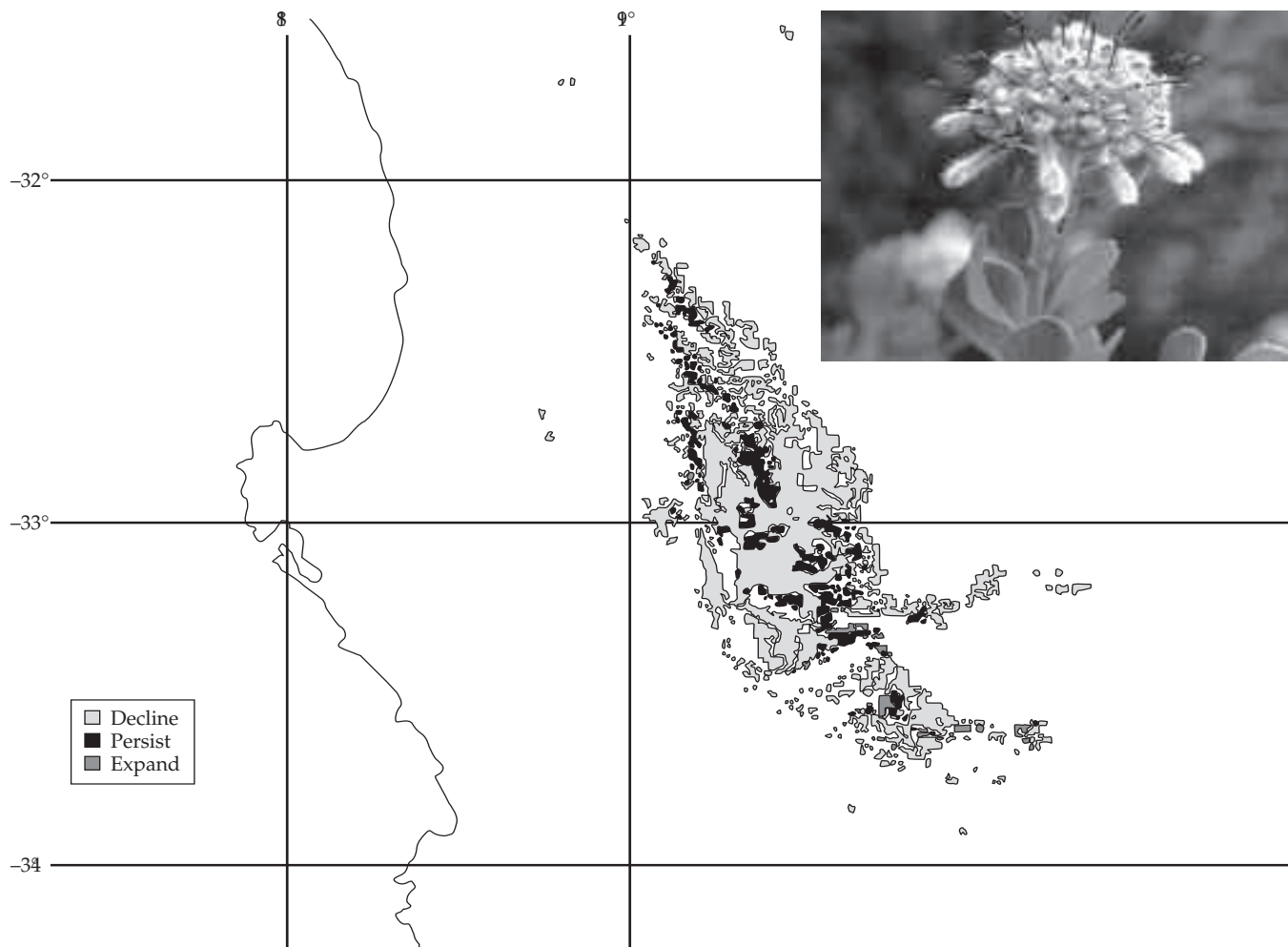
The abundance of zooplankton (microscopic animals and immature stages of many species) has declined by 80% off the California coast. This decline has been related to the gradual warming of sea surface temperatures (Roemmich and McGowan 1995). Zooplankton are a major food source for oceanic wildlife, and the decline of this

food supply has been harmful to many birds, fishes, and mammals. The Sooty Shearwater (*Puffinus griseus*) and Cassin's Auklet (*Ptychoramphus aleuticus*) (which prey directly on zooplankton, or on species that eat zooplankton) have both declined substantially off the central California coast since 1987 (Veit et al. 1996; Oedekoven et al. 2001). However, the Common Murre (*Uria aalge*) remained stable at the same sites (Oedekoven et al. 2001). Though all three species were affected by declines and changes in food resources, their responses were individualistic and apparently related to differences in life histories, foraging behavior, and habitat preferences (Oedekoven et al. 2001).

Clearly, ability to physically track a moving climate zone will be important for species' survival. A very sedentary lifestyle does not bode well for long-term persistence. Unfortunately, many endangered species tend to have just such traits: they have strong local adaptations and habitat specificity, are restricted to small areas, and have limited dispersal ability. An initial "first pass" study as to how such species will fare by 2050 under different climate change scenarios showed that species with low dispersal had nearly twice the risk of extinction of species with high dispersal for any given climate scenario (Thomas et al. 2004).

Scientists use the current distribution of a species to construct a "climate envelope" of threshold values for temperature and precipitation variables within which the species is able to survive and reproduce. These climate envelope models can then be used to estimate what geographic area will be climatically suitable under a variety of climate change scenarios. Figure 10.15 shows the results of one such model for a rare South African flower (Parmesan 2005; Midgley et al. 2002).

The Thomas et al. (2004) study formed its extinction risk estimates by synthesizing results of many different climate envelope models applied to different data sets from around the world. The results provided a rough estimate of extinction risks by 2050. Even if one assumes perfect dispersal capabilities, an absolute reduction in climatically suitable space suggests that about 9%–13% of species could go extinct even with minimal warming



**Figure 10.15** Range shift model of the plant *Vexatorella amoena*, a member of the Proteaceae family whose range is found in the mountains above Cape Town, South Africa. Black denotes range retained in 2050, light gray denotes range projected to be lost in 2050, and dark gray denotes areas in which newly suitable climatic conditions appear for the species in 2050. Gridlines mark latitude and longitude. (Modified from Midgley and Millar 2005.)

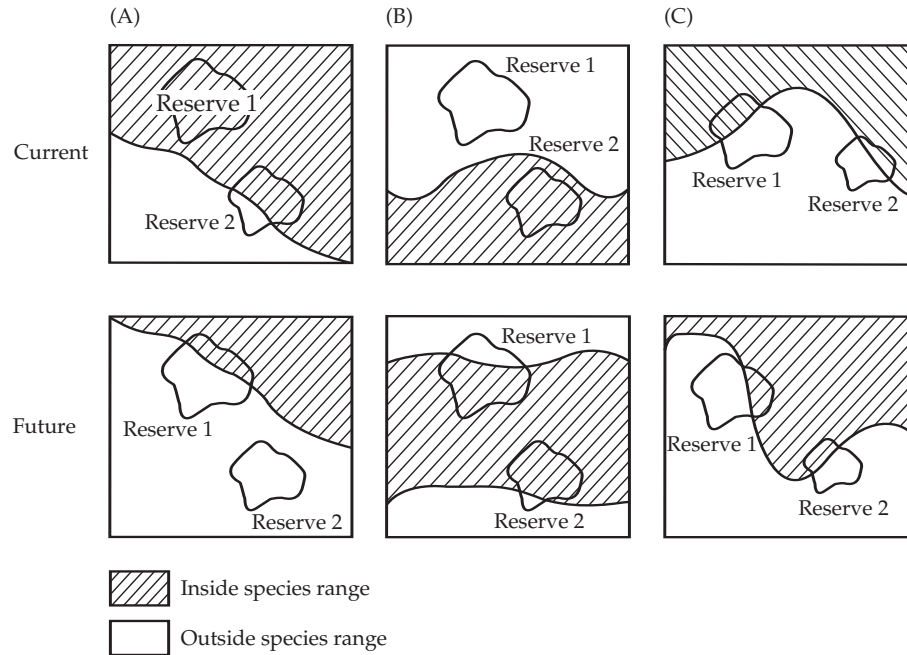
of another 1.2°C (Thomas et al. 2004). Under maximum projected warming (>2°C), extinction estimates varied from 21% to 32%.

The worrying aspect of these estimates is that they are based strictly on climate considerations. However, today's world is fundamentally different than it was during past large climatic fluctuations. Humans dominate the globe. Land has been converted to cities, agricultural fields, or ranching, reducing the quantity and quality of land available for wildlife. The small plots of good habitat that remain are surrounded by wasteland—areas in which most species cannot survive. Species may no longer have the option of simply moving into better environments if the place they are living becomes intolerably hot or dry. Jen-

nifer Gill discusses such subtleties, and describes approaches to predicting changes to coastal habitats and mitigation planning for the conservation of coastal migrant birds in Case Study 10.4.

Current protection of endangered species relies heavily on reserve systems. Often these are a fraction of the species' former range. The concern is that many of these reserves may not remain suitable for the targeted species with another 100 years of climate change. Figure 10.16 shows hypothetical scenarios of a species' climate envelope shifting in and out of existing reserves in the future. Thus species today are much more likely to go extinct than during the Pleistocene if global warming trends continue.

**Figure 10.16** Changing relationships between reserve boundaries and a species' range as climate changes. (A) Decreasing range of the species within a reserve and its absence where it was formerly present; (B) decreasing range of the species within a reserve and its presence where it was formerly absent; (C) change in the location of the species' range. (Modified from Hannah et al. 2005.)



The promises and dangers of a shifting climate are hard to predict for any particular locality. For instance, climate models give conflicting predictions on temperature and precipitation changes for the U.S. Gulf Coast States (Twilley et al. 2001; U.S. National Assessment Report 2001). The only change we can be sure of is that the Gulf Coast is likely to be heavily affected by elevated sea levels.

Though exact prediction may be difficult, (if not impossible), it's clear that the conservation implications are serious. Policymakers, conservation biologists, and resource managers in each state will have various needs and responses to local climate change. Although unique local responses will have to be formulated to address specific localities and conditions, there are some general guidelines that may help in conceptualizing broad strategies.

### **Responses to climate change by resource managers**

Most resource managers and conservation planners focus on local-scale projects such as a particular reserve, habitat, population, or community. Much of their work involves projecting population trends of endangered or threatened species and developing (and then implementing) strategies to stabilize these populations (see Chapter 12). Climate shifts present a new challenge for resource managers because most population models have assumed climate (but not weather) to be an ecosystem constant. With a stable environment, our standard approaches to conservation (e.g., the delineation of fixed areas, protection of rare species, habitat restoration and creation) may be sufficient to maintain biodiversity in

most areas. But climate change could reduce the utility of many of these standard techniques. Resource managers clearly need accurate predictions of local climate impacts. Unfortunately, the same climate models that are reasonably predictive and useful for global planning are poorly resolved at regional levels and are almost nonexistent at local levels. Worse, finer-scaled models may be a long time in coming, and the credibility of such high-resolution forecasting will take yet more time. In the meantime, the climate is already shifting at the local scale.

Fortunately, steps can be taken to minimize the negative impacts of future climate change. Rather than expecting climate scientists to present a specific set of predictions to create a targeted set of responses, local-scale resource managers could develop programs that emphasize flexibility and multiple contingencies. Such an approach fits well with the philosophy of adaptive management that became popular in the early 1990s (see Chapter 13). Some examples of climate-aware adaptive approaches include:

1. The reassessment of species and habitats in regard to their relative vulnerabilities to climate change: An evaluation of the vulnerability of an endangered species, for instance, may differ under scenarios that assume a stable versus a changing climate. Attention and resources may need to be reallocated based on such a susceptibility analysis.
2. The design of new reserves to allow for shifts in the distributions of target species within reserves:

Such shifts may be horizontal (allowing species threatened by rising sea levels, for instance, to move farther inland) or vertical (allowing species to move upward in elevation). An awareness of the need for escape corridors is leading some resource managers to place more value on selecting reserves with great topographic and elevational diversity.

3. The promotion of native habitat corridors between reserves: Corridors along fence lines, ditches, streams, and other minimally used land can aid the redistribution of species between reserves.
4. The creation of dynamic rather than static habitat conservation plans: Management plans based on empirical approaches and regular observation and reassessment are likely to be more useful than detailed long-term scenario modeling given the poor resolution of climate models at local scales. Localized studies of rainfall and temperature trends, regional sea level changes, or shifts in the presence and persistence of vernal ponds are studies that could have important implications at a local level. Moreover, traditionally defined researchers in universities and other large institutions may not be aware of local-scale projects that would be amenable to research designed to address management plans. Local managers may be the best personnel to define, plan, and carry out projects to distinguish between alternate management approaches.
5. The alleviation of the effects of nonclimate stressors: Current climate change is occurring in the context of other anthropogenic stressors (e.g., habitat destruction, industrial contaminants, and invasive species), so the fate of one population will hinge on the net effect of all stressors. In some cases it may be easiest to reduce the overall stress on a species by mitigating some of the non-climate stressors. For example, if both climate change and an invasive species threaten a native population, the most cost-effective approach may be to focus attention on reducing the incursions of the invasives.
6. The generalization of regional or global climate impact predictions to a particular system: Many estuaries, for instance, will face a rapid loss of shallow submerged habitats and low-lying terrestrial habitats with rising sea levels. Increases in the frequency and severity of coastal storms could also cause increased erosion along shorelines and the loss of rookery islands. Salt-intolerant ecosystems such as bottomland hardwoods may face unprece-

dent ed intrusions of brackish waters. More detailed modeling may predict the relative amount or frequency of coastal flooding. On the other hand, current models already make clear that such flooding is going to occur worldwide. A prudent approach therefore, would be to begin preparing for elevated sea levels sooner rather than later.

Specific and detailed local-scale models are vital for resource managers to develop research-based management plans. But in lieu of such models, the above strategies are necessary compromises. Indeed, many resource managers are employing multiple approaches simultaneously. For instance, The Nature Conservancy has been attempting to prepare for climate change in the Albemarle River estuary in North Carolina and Virginia by purchasing “escape zones” upstream along major waterways (see Case Study 10.3). This strategy is designed to give threatened ecosystems buffer zones, thereby allowing plant and animal species to move inland as sea levels rise. Such an approach gives these sensitive communities time and space to adjust to their new environmental conditions.

### ***Climate change and conservation policy***

The global scale of anthropogenic climate change threatens to exceed any other conservation problem. Land-use changes and habitat fragmentation are devastating, but they operate at smaller scales—from local to regional. The logging of a Costa Rican forest does not obviously alter pelagic bird abundance in British Columbia. The potential extinction of Siberian tigers has no clear connection to subsistence farmers in Central African Republic. In contrast, weather patterns and anthropogenic greenhouse gases do not discriminate national boundaries or regional biomes. Warming trends promise to transform our Earth into an unfamiliar place. Citizens and policymakers worldwide must understand that *global* climate change is a *local* issue everywhere.

The pervasiveness of climate change elevated climate-change science in the early 1980s from the province of meteorologists to an issue of great concern to scientists in many disciplines and to policymakers in many nations. Few other conservation issues have achieved such a cohesive international reaction. The creation of treaties such as the Kyoto Protocol and the formation of international climate change advisory groups represent macro-level responses to global warming trends.

Policy implies planning by governments ranging from cities to nations, but policy can also refer to activity by non-governmental organizations such as conservation and environmental groups, many of which are directly involved in large-scale resource management. Corporations also generate and are guided by policies, and many corpora-

tions are involved in the “carbon economy.” Each type of institution has had a strong influence on developing approaches to confront climate change at a global level.

### ***Responses to climate change at national and international levels***

As a general rule, resource managers at local levels focus on coping with proximal environmental issues. Almost by definition they address the “little” (rather than “big”) picture. Yet, in the case of climate change, large-scale problem-solving strategies are going to be needed to mitigate the impending crisis. There is no quick fix for greenhouse-gas-driven climate change, but solutions for alleviating the worst-case scenario are not a great mystery: Existing carbon sources must be reduced or eliminated, and carbon sinks should be increased wherever possible. The result will be a slower rate of climate change over the coming centuries, which will provide ecosystems (and humans) more time to adjust.

Reduction of greenhouse gas emissions by the largest emitters would be useful in slowing the accumulation of greenhouse gases. The largest emitter of greenhouse gases is the U.S., with about 25% of global emissions created by <5% of the world’s population. This is not only considerably larger than other nations in an absolute sense, but only Singapore and Qatar (both of which are very small countries) have higher per capita rates of emissions than the U.S.

However, the action of any single nation—even the U.S.—would eventually be swamped by the general increase in the rate of emission by other nations, particularly China. Further, because carbon and other greenhouse gases are emitted primarily from automobiles and industrial activity, climate change is also an economic issue. Without coordinating actions by other countries, a drop in U.S. emissions would be made up rapidly by increases in greenhouse emissions from developing countries if they follow the same industrialization pathway as the U.S. Thus, the most useful means of lowering the rate of greenhouse gas emissions is to coordinate the actions of many countries, implementing policy reforms at national and international levels simultaneously.

### ***The role of government in climate change policy***

Climate change policy differs a great deal from other environmental issues because of its global scale and because of its implications for wide-reaching economic adjustments. Current negotiations have used the agreements formed as a result of the Vienna Convention for the Protection of the Ozone Layer as a model. The most relevant of these agreements is the Montreal Protocol. The Montreal Protocol sought to limit the production of industrial chemicals that destroy stratospheric ozone and thus allow more biologically dangerous ultraviolet radiation to reach Earth’s sur-

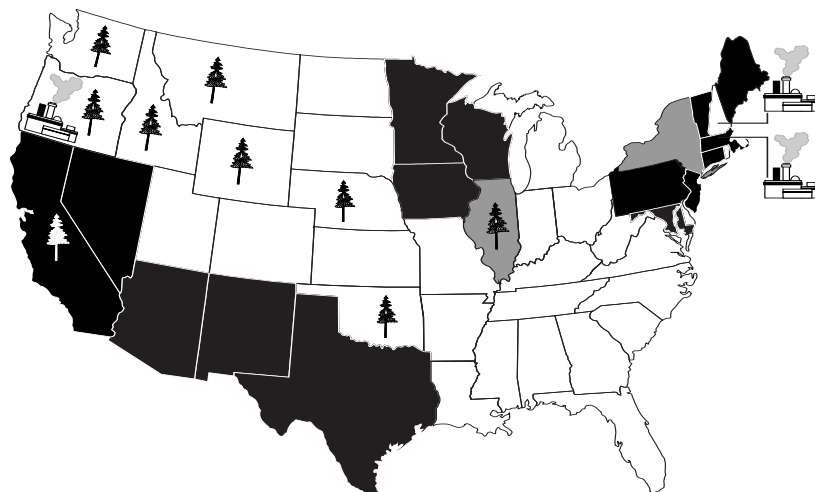
face. The Montreal Protocol has been widely judged a success. Most nations have ratified the treaty, which called for the step-wise elimination of the target chemicals to reduce economic burdens on the industries having to change production methods. The atmospheric concentrations of these chemicals have been greatly reduced, and positive effects in the stratosphere are already apparent. While previous international agreements provide good models, the scope and goals of these earlier treaties were smaller than the issues surrounding climate shifts.

Several differences are notable in contrasting the Montreal Protocol and potential climate agreements. First, the Montreal Protocol focused on families of chemicals that could be replaced relatively easily, but greenhouse gases are produced through processes that permeate our civilization. Reducing emissions of some greenhouse gases such as methane and carbon dioxide will lead to major economic adjustments. In fact, the implications of reducing greenhouse gas emissions on a large scale may be more similar to health care initiatives designed to eliminate smallpox or AIDS worldwide than to the Montreal Protocol. The economic impact of the latter represented little more than tinkering. In contrast, the global strategies to reduce widespread diseases have resulted in the formation of new kinds of global institutions, social structures, and cultural movements that had not previously existed.

Second, the evidence for anthropogenic warming trends is much more complex and relatively less direct than is evidence for anthropogenic damage to the ozone layer. In fact, climate change science could be one of the most sophisticated and multidisciplinary scientific endeavors in human history. Moreover, the records of changes in climate and biological systems are small relative to the impacts predicted for the next few centuries. In other words, policy responses to climate change must be largely based on limited trend data. Definitive proof of catastrophic climate change impacts will not exist until mitigation itself may be too late. Therefore, policymakers are faced with a simple choice: preempt further climate change based on limited information or assume that strong actions can be deferred until later. A brief history of the political process from the time of initial concern to present is described in Table 10.2.

### ***Major themes in climate change negotiations***

Policy debate about climate change made a dramatic shift during the 1990s. In the late 1980s, the scientific basis for ascribing warming trends to human activities still was being formed. Just 10 years later, global leaders were actively working on means of reducing emissions and assessing credit or blame for relative changes in carbon sinks and sources. Many states in the U.S. have already begun programs to curb greenhouse gas emissions (Fig-



**Figure 10.17** Map of states that have programs in place as of September 2003 to reduce sources of greenhouse gases. California is the only state that regulates emissions of greenhouse gases from vehicles. Black indicates states with mandatory energy diversification rules, gray indicates states with voluntary goals toward energy diversification. Power plant icons represent states with mandatory programs to reduce CO<sub>2</sub> emissions from utilities, trees represent states with voluntary forestry or agricultural programs that promote carbon sequestration. (Modified from American Legislative Exchange Council 2002.)

ure 10.17). Climate change is no longer questioned as a process in itself.

The Kyoto Protocol is an outgrowth of the UNFCCC (United Nations Framework Convention on Climate Change) (see Table 10.2) designed to provide specific targets for reductions, reporting of emissions levels, and creation of enforcement mechanisms to ensure that greenhouse gas emissions targets were met. More than 141 nations have ratified the Kyoto Protocol as of February 16, 2005, when the treaty went in force. Despite having broad international support, the Kyoto Protocol was crippled by the withdrawal of support from the U.S. and Russian governments, both of which are actively debating measures that may limit their economies. However, Russian President Vladimir Putin ultimately decided to support the Kyoto Protocol in 2004. It remains unclear how successful the Kyoto Protocol will be without the cooperation of the U.S., the world's largest economy. Still, many nations, particularly in Western Europe, promoted the accord as a vehicle to curbing global greenhouse gas emissions and began the implementation process even without a binding international treaty.

If nothing else, the treaty is the culmination of a broad consensus that developed among scientists and global policymakers that humans are driving changes in the atmosphere that are leading to warming trends and that action must be taken to forestall or slow these trends to avoid social and environmental disasters. However, consensus about how to implement such changes has been even harder to achieve. Several notable themes have played important roles in global talks:

1. Different rules for industrialized versus developing countries: Early in the UNFCCC negotiation process a clear distinction was made between long-industrialized countries (primarily Europe

and other Western nations) and industrializing nations (such as China and India). The former group, also called Annex I countries, are responsible for most of the greenhouse gases currently in the atmosphere; they also tend to be richer than the second group and should be able to bring more technological and economic resources to bear on reducing emissions. The second group of signatories—Annex II nations—are in the process of industrializing; they are likely to contribute more to emissions levels in coming decades. Their economies tend to be less diverse and flexible, often due to their historical relationship with former colonial powers. These nations are given a longer period of time to implement the Kyoto Protocol than Annex I nations. The distinction between “developed” and “developing” countries is likely to remain important in negotiations over the next few decades.

2. Multiple mechanisms for reducing carbon emissions: The Kyoto Protocol is unclear about how emissions would be reduced, although the schedule for emissions reductions is much clearer and more defined (see Table 10.2). Several reduction mechanisms have been proposed. For example, developed nations could replace the use of fossil fuels such as coal and oil with renewable energy sources, such as solar energy, biomethane generators, wind- and water-driven turbines, or nuclear power. Also, both developed and developing nations could reforest areas that had been deforested (thereby creating carbon sinks) and reduce rates of deforestation (which is considered a carbon source).
3. New technologies for old industries: Technological solutions to shifting national economies away

**TABLE 10.2** *A Chronology of Major Climate Change Policy Events*

Date	Meeting or event	Results and conclusions
1896	First attribution of the connection between atmospheric carbon and climate	Svante Arrhenius made the connection between CO <sub>2</sub> and atmospheric temperature and speculated that burning fossil fuels such as coal could increase the concentration of carbon in the atmosphere in the future and lead to an increase in global temperatures. His research was widely disregarded by other scientists at the time.
1979	First World Climate Conference	Human-induced climate change is identified as a potential threat.
1980	Montreal Protocol	World leaders meet to sign an agreement designed to gradually phase out the production and use of chemicals that destroy atmospheric ozone.
1988	Formation of IPCC	The United Nations Environment Program (UNEP) and the World Meteorological Organization (WMO) create the Intergovernmental Panel on Climate Change (IPCC) to coordinate research and analysis of climate change.
1990	First IPCC Report	The IPCC states global climate is clearly changing, and these changes are probably a result of human activity.
1992	Rio Convention	The United Nations Conference on the Environment and Development (also known as the Earth Summit or Rio Convention) convenes in Rio de Janeiro, Brazil. A total of 154 nations sign the United Nations Framework Convention on Climate Change (UNFCCC), which asks signatories to reduce greenhouse gas emissions and creates a feedback mechanism for future talks. Developed nations (also known as Annex 1 countries) will be asked to make larger reductions than developing nations.
1995	Second IPCC Report	The second report states that “the balance of evidence” leads the authors to conclude that there was a “discernible human influence on the global climate system.” New evidence suggests that climate change processes are more serious than they were described in 1990, and the first attempt at reducing human impacts seems weak. Many policymakers and scientists believe the UNFCCC needs stronger teeth.
1995	COP1: The Berlin Mandate	At the first Council of the Parties (COPs) meeting, the Berlin Mandate is signed, which formally recognizes the ineffectiveness of UNFCCC calls for voluntary greenhouse gas reductions. A committee drafts protocols to design other strategies for the 1997 COPs meeting.

from carbon-based systems are likely to increase in importance. One example is the development of cost-efficient hydrogen fuel cells. These fuel cells emit only water vapor but have proven difficult to produce cheaply and on a small scale. Another is the development of low- and no-emission coal-fired electrical generating plants, which would operate by pumping their carbon emissions into long-term storage (“sequestration”) below ground or in the deep oceans. The widespread implementation of either strategy is probably a decade or more away.

4. Fostering incentives to meet targets: Many have advocated making use of market-based tools, including the buying and selling of emissions and reduction “credits.” These credits could be

exchanged between developed nations and between developed and developing nations. In anticipation of global implementation of the Kyoto Protocol, the Chicago Carbon Exchange is already up and running.

Beyond these international efforts, many corporations are making changes on their own. In the petroleum industry, major voluntary shifts in corporate strategy have been taking place, reflecting the influence of public opinion and the future profitability of alternative energy sources. British Petroleum (BP), one of the world’s largest corporate oil producers, recently adopted a widespread marketing campaign stating that BP stood for “Beyond Petroleum” (Wee 2002). Shell Oil Company has shifted research efforts into solar energy technology and

TABLE 10.2 *Continued*

Date	Meeting or event	Results and conclusions
1997	COP3: The Kyoto Protocol	Delegates in Kyoto, Japan, agree that Rio Convention targets are insufficient and emissions should be reduced more quickly. Global emission levels should be 5% less than 1990 levels by 2012, Annex 1 nations are asked to make much more substantial reductions to meet the global figure. The U.S. agrees to a 7% reduction and Canada to 6%; the European Union level is an 8% reduction. Some nations go much farther. Germany promises to reduce emissions by 25% and the United Kingdom by 15%. About 160 nations sign the accord, which must then be ratified or acceded to in each country. The treaty does not become activated until the 1990 emissions levels of ratifying countries totals at least 55% of 1990 levels. At this point, a stepwise series of greenhouse gas emissions kicks in. Greenhouse gas reduction mechanisms will be detailed at COP6 in 2000.
2000	COP6: The Hague, Netherlands	The U.S. under George W. Bush (elected in 2000) and Canada under Jean Chrétien want larger amounts of carbonsink credit for forest growth (thereby allowing for higher net carbon emissions) than other signatories will allow. The meeting fails to negotiate an agreement on mechanisms and breaks up. A second meeting held shortly afterwards again dissolves without an agreement. Since the U.S. is the largest emitter of greenhouse gases worldwide, many observers feel that the Kyoto Protocol will have little impact without U.S. support. The Kyoto Protocol is widely pronounced to be dead.
2001	COP7: Bonn, Germany	Some 180 countries constituting all of the Kyoto Protocol signatories except the U.S. and Australia (but now including Canada) approve the mechanism framework for implementing the accord. Supporters of the Kyoto Protocol focus on pressuring other large emitters (e.g., Russia and Japan) to ratify the treaty.
2001	Third IPCC Report	More sophisticated modeling leads IPCC authors to write “globally averaged mean surface temperature is projected to increase by 1.4° to 5.8°C over the period 1990 to 2100.” The third report also compiles substantial evidence of biotic effects.
2002	Rio + 10: Johannesburg, South Africa	The U.N. World Summit on Sustainable Development follows up on issues raised by the Rio de Janeiro summit in 1992 (hence the conference’s alternate name: Rio + 10), with special attention to finding means to create climate-friendly development.
2004	Moscow	Russia’s president Vladimir Putin ratifies the Kyoto Protocol, which immediately activates provisions of the treaty.
2007	Fourth IPCC Report	Work has begun already to prepare the next scheduled IPCC report, due in 2007.

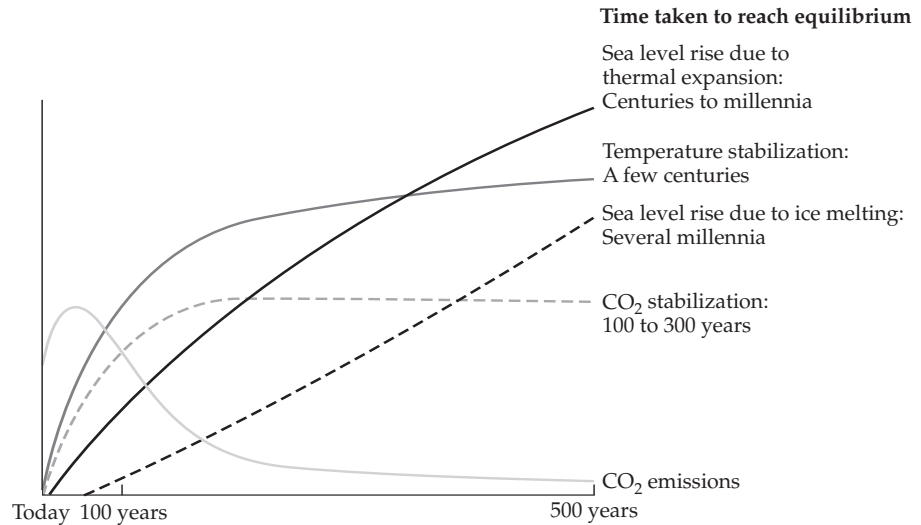
development, and in 2004 Shell’s CEO spoke out on the need for a major shift away from carbon-based fuels to avert the most severe climate change scenarios (Adam 2004). Indeed, alternative energy sources, such as nuclear, solar, and geothermal, have been an important area for research for many oil companies since the OPEC oil crisis of the 1970s, though these shifts are only small components of the portfolio for most of the large petrochemical producers and refiners even today. Nonetheless, voluntary shifts in corporate policies (see Figure 10.16) will continue to play an important role in climate outcomes and global climate policy.

**The future of climate change policy**

Regardless of what policy actions are taken, Earth’s ecosystems have already made a commitment to climate

change. In other words, even if all greenhouse gas emissions ended immediately, the rise in atmospheric CO<sub>2</sub> that has already taken place will continue to warm Earth for another century (Figure 10.18). The 1990s will probably be remembered as a decade when scientists and policymakers in most nations moved from simply expressing concern about climate change to beginning to commit to action. The relevance of these actions to conservation biology is in many cases indirect: Most policymakers are acting out of concern for the effects of climate shifts on humans rather than ecosystems. On the other hand, the UN-FCCC accord may be an example of an instance in which actions taken for the good of human societies are also good for ecosystems. Certainly the foresight that the UN-FCCC and the Kyoto Protocol reflect bodes well for continued co-existence of humans and natural biodiversity.

**Figure 10.18** Projected rise in global mean temperature over the next 100 years depicts Earth's "commitment to climate change." This figure is a generic illustration for CO<sub>2</sub> stabilization at any concentration between 450 and 1000 ppm, and therefore has no units on the response axis. Responses to stabilization in this range show broadly similar time courses, but the impacts become progressively larger at higher concentrations of CO<sub>2</sub>. After CO<sub>2</sub> emissions are reduced and atmospheric concentrations stabilize, surface air temperature continues to rise by a few tenths of a degree per century for a century or more. Thermal expansion of the ocean should continue long after CO<sub>2</sub> emissions have been reduced, while melting of ice sheets should contribute to sea level rise for many centuries. (Modified from IPCC 2001c.)



## CASE STUDY 10.1

### Challenges to Predicting Indirect Effects of Climate Change

Lisa Crozier, University of Chicago

This chapter demonstrates that climate change has widespread, profound, and complex effects. Here, I explore the theme of complexity. We can currently only glimpse at the depth of ecological and evolutionary understanding that is necessary to predict the biological changes to come. We know that the delicate web of ecological interactions as they exist now will be disrupted by rapid climate change, but predicting where strands will break and where new strands will be spun is extremely difficult. Each species will experience both direct effects of climate change (e.g., temperature or desiccation stress), and indirect effects that are mediated through some secondary physical or biological process (e.g., a shift in ocean currents or a change in a predator–prey interaction). Our current experimental approaches are adequate for predicting direct effects, but indirect and synergistic effects are much less tractable. These secondary effects are therefore poorly understood, and so are not included in most predictions despite evidence that they can overwhelm direct effects. Much work lies ahead to unravel the many ties between species and their environments and to clarify how behavioral or physiological processes may change in response to a changing environment.

Consider a forest ecosystem. Tree growth and survival are very sensitive to temperature, precipitation, and potentially

CO<sub>2</sub> concentration (i.e., direct effects). However, they are also very sensitive to disturbance regimes and herbivory (i.e., indirect effects). Climate strongly influences the frequency, intensity, and nature of major disturbances that in turn shape both species composition and ecosystem function. A change in disturbance regimes can transform communities much faster than changing temperatures alone. Major disturbances hasten the death of increasingly maladapted genotypes and open up large areas to colonization by different species. Herbivores large and small can also tilt the competitive balance between plants, and herbivores will respond directly to climate change as well as to changes in plant condition and predation rates. How will all of these dynamics interact over the next century?

#### Changing Disturbance Regimes Will Change Communities

Disturbance regimes such as fire and insect outbreaks are now recognized as an essential characteristic of many communities. Different species are adapted to different fire regimes. Spruce (*Picea* sp.) and juniper (*Juniperus* sp.), for example, cannot tolerate frequent fires, whereas lodgepole pine (*Pinus contorta*) depends upon fire to replace itself. The frequency, seasonality, severity, and type of fire (e.g., crown or surface) determine

postfire ecosystem structure and function (Flannigan et al. 2000). These qualities in turn depend on existing forest characteristics and climate. Fires will likely increase in severity and frequency over most of North America due to rising temperatures and more variable precipitation (Flannigan et al. 2000). This increase is expected even in some regions where average precipitation goes up, because wet years foster rapid growth and produce extra fuel that burns more intensely during dry years. Fire-tolerant species will be favored in these regions. These species in turn tend to promote fires (e.g., by having more flammable wood). Concern is growing that fires may establish a positive feedback loop and contribute to global warming by releasing stored carbon, changing reflectance properties and reducing evapotranspiration rates (Dale et al. 2001). So warming begets fire, which begets fire-loving trees that beget more fires, which beget more climate warming, and the cycle repeats itself.

Insect and pathogen outbreaks also shape plant communities. Insects and pathogens are actually the dominant force of disturbance in forests in the United States, as measured by area affected (20.4 million ha/year) and economic cost (U.S.\$1.5 billion/year) (Dale et al. 2001). Outbreaks predispose some forests to major fires by increasing fuel load, providing fallen trees that act as "fire ladders" which convert surface fires to stand-killing crown fires, and providing smoldering material that eventually spreads when weather conditions are suitable (Logan and Powell 2001). Outbreaks also often occur when trees are drought stressed (Mattson and Haack 1987), which tends to occur in hot, dry years when fires are more likely. Tree-ring chronologies show that insect outbreaks have been a regular feature of forest life for thousands, and probably millions of years (Swetnam and Lynch 1993). Like fire, these so-called "normative outbreaks" are necessary for the regeneration of some forests (Mattson 1996; Logan and Powell 2001). Nonetheless, severe outbreaks can cause essentially permanent changes in vegetation, especially when conditions for regrowth are somewhat less favorable than average. For example, several large outbreaks of the autumnal moth, *Epirrata autumnata* in northern Europe transformed patches of dense birch forests into tundra (Kallio and Lehtonen 1973). Climatic factors probably contributed to both the outbreaks and poor regrowth. Reindeer and vole herbivory further hindered regeneration. An even greater concern is that as insects shift ranges they may colonize new hosts that cannot tolerate large-scale infestations.

Outbreaks will probably increase in many areas where they are now infrequent. Warmer winters increase outbreak probability in species such as the autumnal moth (Virtanen et al. 1998) and southern pine beetle (*Dendroctonus frontalis*) (Ungerer et al. 1999) by increasing overwinter survivorship. Outbreaks in other species, such as spruce beetle (*D. rufipennis*) and mountain pine beetle (*D. ponderosae*), depend on the amount of time it takes for larvae to complete their life cycle, and this time period depends on temperatures during the growing season (Hansen et al. 2001; Logan and Powell 2001; Regniere and Nealis 2002).

As temperatures rise, these species will invade higher latitudes and elevations. Other species, such as gypsy moth (*Lymantria dispar*) and spruce budworm (*Choristoneura occidentalis*) will respond more to changes in precipitation (Williams and Liebhold 1995), so it is difficult to predict whether outbreaks will increase or decrease because of uncertainty in climate forecasts.

Because most species have survived warmer climates in the past, theoretically they should not be threatened by outbreaks of native insect species. However, some defoliating insects are introduced (such as the gypsy moth), so climate change will expose naive hosts to attack. Furthermore, if trees are weakened by other stresses or have greatly reduced habitat, they may be much more vulnerable. For example, whitebark pine (*Pinus albicaulis*) may be seriously threatened in the Rocky Mountains by climate-induced shifts in the range of the mountain pine beetle (Logan and Powell 2001). Whitebark pine has been decimated by an introduced blister rust throughout much of their historical range, so the remaining healthy populations are important for the species' survival. Mountain pine beetle will likely invade whitebark pine habitat in response to a 2°C rise in temperature. Whitebark pine is a very long-lived species, with some individuals reaching 1500 years old. Its life history strategy makes it unlikely that it could recover quickly from defoliating outbreaks. Decline of whitebark pine would affect the entire ecosystem because it provides essential food resources for many species. Its pine nuts are especially high in fat, making them the preferred food source of the mutualist bird, Clark's Nutcracker (*Nucifraga columbiana*), red squirrels, and bears. Grizzly and black bears raid squirrel pine nut caches in preparation for hibernation, when accumulating fat reserves is especially important (Mattson et al. 2001). These long-lived hardy trees also provide ecosystem services such as snow stabilization, which helps store water for the thirsty west.

### Trophic Interactions Askew

Many of the predictions above are based on the direct effects of temperature on insect survivorship or growth rates. However, insect responses may be tempered by interactions with other species, such as host plants or predators. For example, it is important for many caterpillars to emerge from winter dormancy at the same time as their host plants. If caterpillars emerge from winter dormancy too early, they may starve before their host plants leaf out. On the other hand, if caterpillars emerge too late, they miss the more nutritious and palatable young foliage. However, each species has a unique set of cues that trigger seasonal behaviors, so synchrony between host plant and herbivore may not be maintained during climate change. For instance, egg hatch in the winter moth, *Operopthera brumata*, depends on cumulative temperatures above a certain threshold, and therefore responds directly to warmer springs by hatching earlier. One of its host plants, Sitka spruce (*Picea sitchensis*), on the other hand, depends on a chilling period in addition to accumulating spring temperatures to trigger budburst. When warmer winters reduce chilling, the spring temperature

threshold rises, delaying budburst. So the asynchrony between caterpillar emergence and spruce budburst is expected to grow in response to climate change (Dewar and Watt 1992). Another host plant for this species, red oak (*Quercus rubra*), does not have a chilling requirement so its budburst has advanced in recent years—but the response has been slower than that of the winter moth (Visser and Holleman 2001). The suitability of various hosts may therefore change with climate change. However, in most cases we do not know exactly what triggers each species, so many pair-wise interactions are hard to predict (Harrington et al. 1999).

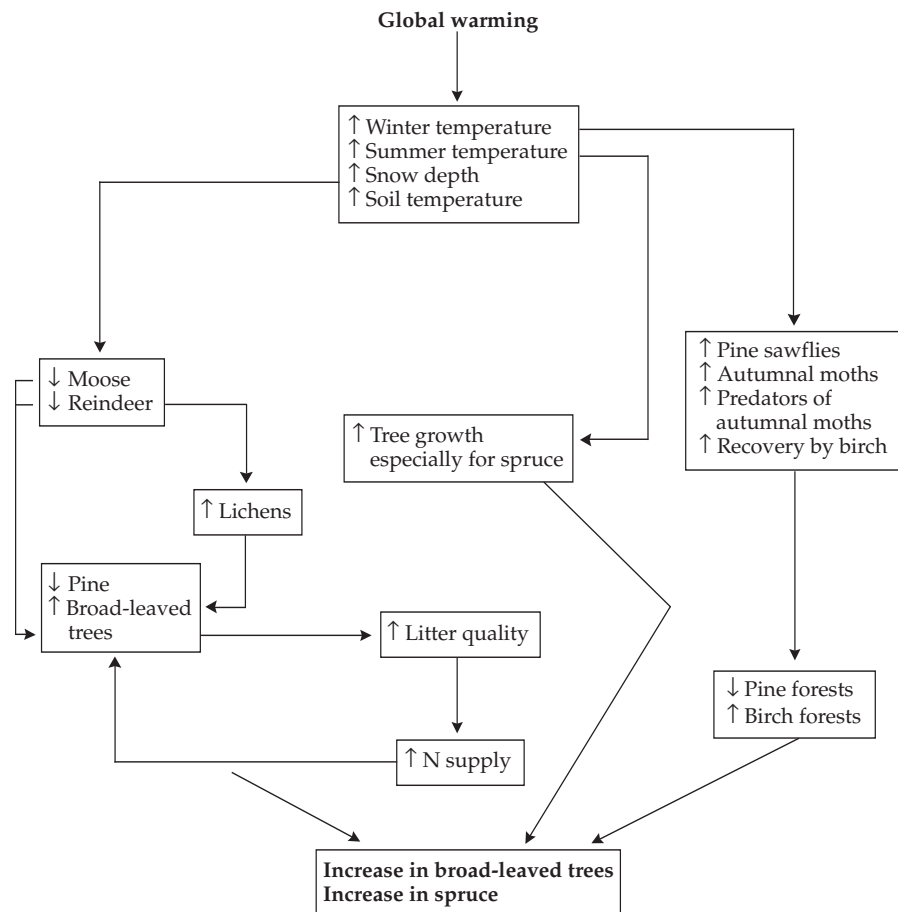
Predators of insects will also vary in their responses to climate change and their ability to track changing phenology of their prey. Parasitoids are often limited more by cool temperatures than are their prey (e.g., Randall 1982, Davis et al. 1998, and Virtanen and Neuvonen 1999), so warming will increase their relative impact. However, birds seem to be less flexible in advancing their migrating and breeding behaviors to keep up with earlier caterpillar emergence (Van Noordwijk et al. 1995; Visser and Holleman 2001; Strode 2003; Visser and Rienks 2003). Migrating birds face an even greater challenge in trying to maximize food availability at multiple stops along their migration route, because warming is occurring much more rapidly at higher latitudes (Strode 2003). Determining the limiting factors for each of these species individually and then in concert with changes in other species is a daunting task, but is essential for predicting how they will respond in years to come.

### Comparing Direct and Indirect Effects in Boreal Forests

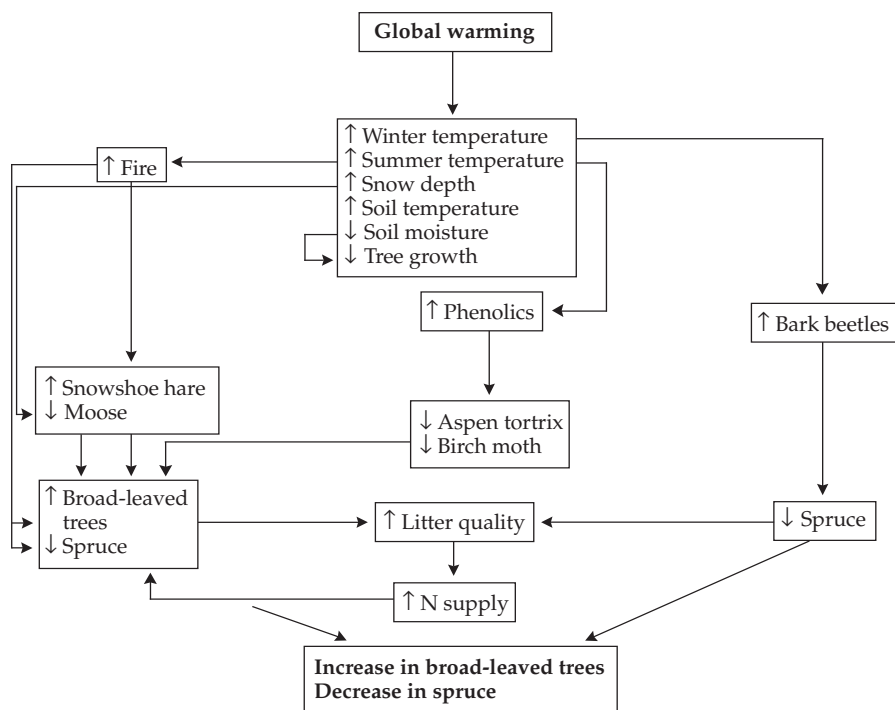
With all species responding independently to climate change and to each other, how can we hope to predict the net effects? It is extremely difficult and few authors have tried it. A comprehensive understanding of community interactions is needed, and few ecosystems have been studied thoroughly enough to achieve this level of understanding. Nonetheless, to demonstrate the potential importance of indirect effects, Niemela et al. (2001) attempted such an analysis of boreal forests (Figure A). They predicted that in some cases the effects of herbivores and secondary changes in soil quality will outweigh the direct effects of climate change on vegetation. For example, in southern Finland,

Norway, and Sweden the direct impacts of climate change are likely to be minimal because the dominant trees are relatively insensitive to changes in winter temperature, and little change in summer temperature or precipitation is predicted for this region. Insect and mammalian herbivores however, are extremely sensitive to winter temperature and precipitation. Snow depth has a strong impact on foraging success of moose (*Alces alces*) and deer, and consequently their winter survivorship (Ayres and Lombardero 2000; Niemela et al. 2001). Because browsing mammals tend to prefer broad-leaved species, their success is likely to convert a neutral tree response to a negative one. These authors predict that pine sawflies (*Nediprion sertifer*) will have a greater impact on pine, while moose and roe deer (*Capreolus capreolus*) inhibit the growth of broad-leaved trees. In sum, increased herbivory on competitors will lead to an expansion of spruce.

Farther north, the direct effects of climate change should improve growth of spruce, pine, and birch. The expected rise in snow will be deleterious for moose and reindeer, but rising winter temperatures should be advantageous for the autumnal moth and the pine sawfly. Because these moths limit birch and



**Figure A** Effects of climatic warming on the biotic interactions likely to influence forest composition in northern Finland, Norway, and Sweden. (Modified from Niemela et al. 2001.)



**Figure B** Effects of climatic warming on the biotic interactions likely to influence forest composition in interior Alaska. (Modified from Niemela et al. 2001.)

pine, respectively, they would be expected to counteract benefits for both birch and pine. However, increasing ant predators of the autumnal moth and improved growing conditions for birch may compensate for insect damage in birch, but not in pine. Overall these authors predicted that both spruce and broad-leaved species will increase in the north. In Alaska, on the other hand, fire and bark beetles are expected to shift the advantage to broad-leaved species (Figure B).

Clearly, incorporating many species interactions into our predictions radically complicates forecasts. All of the pair-wise dynamics mentioned above are well documented, but extrapolation to the whole ecosystem is still somewhat speculative. Experiments at the ecosystem scale are very difficult, so these predictions require careful extrapolation from small-scale experiments, and specially designed factorial experiments. Furthermore, predictions are even more difficult because most of the traits of interest could change over time.

### Evolutionary Potential and Constraints

A crucial assumption underlying the examples discussed above is that preferences and tolerances are constant. However, most of these traits can change, as demonstrated by artificial selection experiments in the lab, geographic variation in the field, and changes in natural populations over time. Plastic behaviors and the potential for genetic change in response to climate change are hardest to predict because they require extensive experimentation and some inherently unpredictable events.

Many of the behaviors that determine phenology are under genetic control, and therefore would require evolutionary change to maintain synchrony between trophic levels. Evolution in these traits can happen very quickly, as demonstrated by the recent change in day length necessary to induce dormancy in the pitcher plant mosquito (*Wyeomyia smithii*) (Bradshaw and Holzapfel 2001). This mosquito has adapted over the past 30 years to a longer growing season by requiring a shorter day to trigger winter hibernation. Cues for hibernation are finely tuned along latitudinal gradients in many species, so these traits are probably very labile (Bradshaw 1976; Scriber 1994; Chown et al. 2002). However, this flexibility may be the exception rather than the rule. Constraints on evolution can be subtle, reflecting the underlying genetic architecture of phenotypic variation. In a spectacular study of genetic constraints on adaptation to global warming, Ettersson (2001) demonstrated that evolution of drought tolerance in prairie plants in Minnesota may be slowed by links between genes.

Genes associated with traits that would be advantageous in a more arid environment are tied to other genes under different (sometimes opposing) selection pressures. Large-scale transplant experiments with complete genetic crosses like this are extremely difficult, but they reveal fundamental constraints many species may face.

Additional constraints have been imposed by humans. Rapid evolution requires genetic variation for the relevant trait, which is diminished in very small populations or populations that have been selected by humans for particular traits. For example, stress tolerance is frequently associated with slower growth rates, so forestry practices that select for faster-growing trees have reduced natural variation that would have facilitated adaptation to climate change. Highly fragmented and reduced habitat also lowers the chance that individuals will find suitable areas for colonization outside their current ranges, which will be necessary as suitable climates move to higher latitudes. Thus although ecological and evolutionary responses may have allowed species to survive previous climate changes, resilience to future changes is much less certain. Like most of the other anthropogenic impacts discussed in this book, disrupting Earth's climate is a massive and irreversible experiment. The results will not be known for decades or centuries, so we must rely on our predictions to decide how we should act now. Large pieces of the puzzle are still missing, but we can greatly improve our understanding by incorporating indirect effects into more ecological and evolutionary studies.

## CASE STUDY 10.2

### Climate Change, Extinction, and the Uncertain Future of a Neotropical Cloud Forest Community

Karen L. Masters, Council on International Educational Exchange, J. Alan Pounds and Michael P. L. Fogden, Golden Toad Laboratory for Conservation, Monteverde Cloud Forest Preserve and Tropical Science Center

Steep mountainsides in northern Costa Rica rise into the clouds and spread along a northwest–southeast axis, which bisects the land into two climatically distinctive regions. The mountaintops, obscured from sight by billows of blowing mist, are carpeted by verdant cloud forest. Just below the bank of clouds, on the Pacific slope, abundant sunshine pierces the blowing mist and ignites rainbows that arc overhead, recalling the legend of the pot of gold at the rainbow’s end. The world-renowned Monteverde Cloud Forest is indisputably wealthy in biodiversity: Monteverde’s bank of biological richness includes some 3000 species of vascular plants (Haber 2000), more than 160 species of reptiles and amphibians (Pounds 2000), and 425 resident or migratory bird species (Young and McDonald 2000).

Straddling the continental divide along the Tilarán mountain range in northern Costa Rica, Monteverde is bathed in clouds nearly year round because of two distinctive oceanic weather systems, Caribbean and Pacific, which maintain the cool, lush conditions on the mountaintop (Figure A; Clark et al. 2000). A nearly perpetual supply of nutrient-rich precipitation supports record loads and diversity of epiphytes (plants that live on top of others), including orchids, ferns, and mosses, giving the vegetation its characteristic look and feel. Fre-

quent rainfall and leaching produce nutrient-poor soils and encourage the epiphytic growth form as well as the stilt roots of many cloud forest trees, beneath which golden toads (*Bufo periglenes*), now extinct, once gathered to breed. The almost continuous input of moisture results in relatively high plant productivity year round, yielding reliable resources for myriad organisms, such as Resplendant Quetzals (*Pharomachrus moccino*), which migrate locally between patches of fruiting trees (Powell et al. 2000).

Their dazzling colors and courtship, along with their care of young, nestled in cavities of old snags, engage a booming tourist industry and fascinate field biologists. However, when decades-long research on Monteverde bird communities revealed that the Keel-billed Toucan (*Rhamphastos sulfuratus*), a known predator of hole-nesting birds and a resident of lower elevations, had colonized and begun breeding in cloud forest habitat, ornithologists questioned why this was happening. The Keel-billed Toucan was not unique: Many other cloud forest intolerant bird species were showing similar upslope shifts in breeding ranges. Simultaneously, herpetologists were becoming increasingly concerned by downward trends in populations of lizards, and were alarmed by the outright disappearances of once-abundant frog and toad species, including two—the golden toad (*Bufo periglenes*) and Monteverde harlequin frog (*Atelopus* sp.)—that were endemic to Monteverde (Pounds 2000; Pounds and Puschendorf 2004). Sharing notes and concerns, biologists began to explore possible explanations for the emerging patterns.

Habitat loss was quickly ruled out because forest regeneration was common in the Monteverde area. The spread of pathogens, while perhaps affecting specific taxa, seemed an unlikely universal explanation, given the range of species involved. Researchers began to investigate local climate and the impacts of large-scale events and processes such as El Niño and global warming. Evidence in favor of a shifting local climate, brought about by global warming but punctuated by El Niño events, is mounting; climate shifts now figure prominently as the ultimate cause of the biological changes. Indeed, it is increasingly clear that the demise of the golden toad and that of the Monteverde harlequin frog represent the first, modern-day extinctions linked to global warming.

Monteverde’s climate has changed profoundly since 1972 when John H. Campbell, an original Quaker settler of the zone,



**Figure A** Cloud cover over mountainous regions of Costa Rica are necessary for development of cloud forest ecosystems. (Photograph courtesy of Andrew Sinauer.)

began collecting daily weather data (Pounds et al. 1999). The frequency of days with little or no measurable precipitation during the windy-misty and dry seasons (December to May) has increased. Moreover, while the total precipitation during this period has not changed, precipitation is now concentrated on fewer days, yielding longer stretches of mist-free or mist-reduced days (Pounds et al. 1999). Whereas sequences of three or more dry days were rare in the 1970s, it is now common to have stretches of five or more days with dry or near-dry conditions.

According to the lifting cloud base hypothesis, the altitudes at which clouds form as air masses ascend the mountain slopes has increased, reducing moisture inputs to the cloud forest (Pounds et al. 1999). In a warming world, both the rate of evaporation and the water-holding capacity of air increase, thereby enhancing the water vapor available for cloud formation (IPCC 2001a). However, the altitudes at which clouds form depend on local conditions of relative humidity and thus on temperature (Still et al. 1999).

The frequency of cloud cover has also increased. Clouds reduce incoming solar radiation while having an insulating effect at night. An increase in nighttime temperatures and a decrease in daytime temperatures have reduced the diurnal temperature range, the difference between the daily minimum and the daily maximum (Pounds et al. 1999). All of the above parameters are linked to large-scale climatic conditions, including global warming and El Niño events. Over the past 30 years, global sea surface and air temperatures have risen sharply (IPCC 2001a). Together with the superimposed warm episodes of El Niño, the trend has led to more frequent and longer dry spells at Monteverde (Pounds et al. 1999).

Diverse vertebrate taxa, including amphibians, reptiles, and birds, have variously responded to climate change at Monteverde (Pounds et al. 1999). The most famous cases involve the extinctions of two local endemics, the golden toad and the Monteverde harlequin frog. In the same period, local populations of 20 other amphibian species disappeared. While a few have recolonized, post-crash censuses show that populations have fluctuated in response to climate but have remained below pre-crash densities. In the case of reptiles, local populations of the cloud forest anole (*Norops tropidolepis*) and the montane anole (*N. alatae*), both endemic to Costa Rica, have declined since the late 1990s, when amphibian populations first fell dramatically (Pounds et al. 1999). In contrast, the gray lichen anole (*N. intermedius*), previously limited to middle elevations, has now colonized upper regions, and the ground anole (*N. humilis*), a primarily lowland species, has increased in abundance.

Upslope colonization is better documented for bird communities, which have been extensively studied since the late 1970s. Numerous cloud forest intolerant species have extended their ranges upslope, while most cloud forest species have not altered their distribution (Pounds et al. 1999). The net colonization rate (the number of species moving up minus the number moving down) is positive in some years and negative in others, as it fluctuates with climate. Nevertheless, the aver-

age colonization rate is positive, indicating an overall pattern of upslope range extension. Compositional changes in the bird community are pervasive and striking; colonizing species represent broad taxonomic and ecological ranges from both the Atlantic and Pacific slopes (Pounds et al. 1999).

The taxonomic diversity of affected species and the variety of reactions suggests multiple proximate triggers, all linked by sensitivity to climate change. Amphibian declines worldwide have directed attention to possible taxon-specific explanations that may not easily apply to birds and reptiles at Monteverde, but may be ultimately linked to climate. For instance, the chytrid fungus *Batrachochytrium dendrobatidis*, which attacks the skin of amphibians and may under some circumstances cause mortality, is a suspected culprit in the extinction of amphibian populations (Berger et al. 2004). Pounds and Puschendorf (2004) hypothesize that increasing cloud cover may prevent chytrid-infected frogs from raising their body temperatures sufficiently to kill the fungus, thus facilitating its persistence and transmission. This hypothesis, like others that propose climate-mediated disruptions in host-parasite interactions, has not been tested. Nevertheless, it highlights the importance of species interactions and the complexity of biological response to climate change (Pounds 2001). Clearly, investigations into the proximate mechanisms of Monteverde extinctions and population declines are of pressing significance.

The observed patterns signal ongoing or imminent change in both the biotic and abiotic elements of the Monteverde cloud forest. Although Neotropical cloud forest plants adapted to the climate oscillations of the Pleistocene, the current temperature increase may be ten times faster than that during the transition from the Pleistocene to modern times (Bush et al. 2003). Increased rates of extinction are a likely consequence. The Monteverde case suggests that range-restricted or dispersal-limited species, or those adapted to narrow environmental conditions or interacting with such species will suffer most. Climatic specificity for narrow altitudinal ranges often characterizes tropical montane organisms, especially cloud forest species.

Cloud forest epiphytes may be especially vulnerable (Figure B). Many are climate-sensitive (e.g., Gentry and Dodson 1987; Benzing 1995, 1998; Atwood 2000), having adapted to particular conditions within the high microclimatic heterogeneity that characterizes cloud forests (Lawton and Dryer 1980; Clark and Nadkarni 2000; Haber 2000; Haber et al. 2000; Kappelle and Brown 2001). In the Monteverde area alone, there are over 500 species of orchids, many of which inhabit narrow altitudinal belts according to their specific temperature and moisture requirements (Atwood 2000; Hammel et al. 2003). Critical to ecosystem functioning of cloud forests, epiphytes are both "nutrient scavengers," taking up compounds in mist that would otherwise blow by the canopy, and keystone species, by providing nutrition to diverse organisms throughout the year (Coxson and Nadkarni 1995). Thus, losses of epiphytes may have consequences that reverberate through all trophic levels.



**Figure B** An epiphyte such as this orchid *Encyclia ionophlebia*, is an important component of cloud forest ecosystems. (Photograph © Oxford Scientific/photolibrary/Michael Fogden.)

Species that successfully adapt to ongoing change at Monteverde or that colonize the area will create non-analog communities. The composition of these communities will depend on the climatic tolerances of species and their ability to adapt to novel interactions. Rates of community transformation may exceed those at which interacting species can adapt to one another, leading to disruptions, for instance, in natural host–parasite population cycles. Whether and how native species will cope with simultaneous changes in climate and community composition is unclear. For instance, the Resplendant Quetzal, whose altitudinal distribution rarely includes the comparatively low elevations of Monteverde (Stiles et al. 1989), is already declining (Fogden, unpublished data). Whether it can survive as communities continue to change is doubtful. What seems likely is that the singular character and quality of the Monteverde cloud forest, assembled of unique species that have evolved over the millennia in response to one and other and to the physical environment, will be forever transformed in a matter of decades.

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## CASE STUDY 10.3

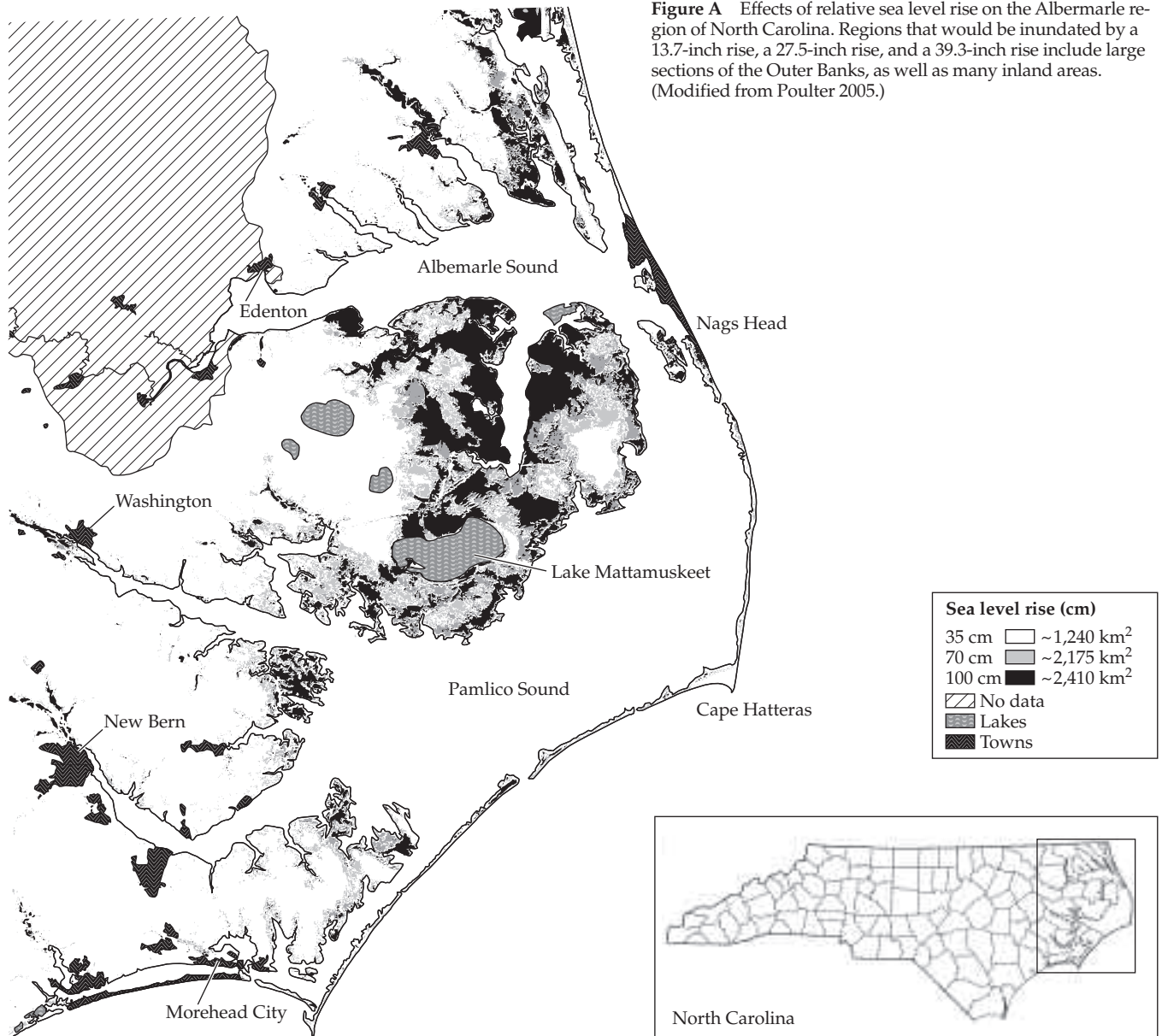
### Adapting Coastal Lowlands to Rising Seas

*Sam Pearsall, The Nature Conservancy and Benjamin Poulter, Duke University*

In the Albemarle Region of northeast North Carolina (Figure A), the land is subsiding and the sea is rising. Global warming from post-industrial modification of the atmosphere is causing the sea to rise, partly as the result of ice melting, but mainly due to the thermal expansion of seawater. In the Albemarle Region, the current, combined rate of relative sea level rise is 43 mm (2 inches) in 10 years (Permanent Service for Mean Sea Level 2004), and when the sea rises an inch, it extends inland many feet. Forty inches of sea level rise will inundate about a million acres of low-lying lands (see Figure A). At the present rate, this will take 200 years. If the rate triples, it will take about 65 years, less than a lifetime.

Rising seas produce adverse environmental effects locally as the result of inundation, salt poisoning, and erosion. If the Outer Banks are breached by hurricanes that are stronger and more numerous, then the local effects could be severe. The effects of rising seas also may be felt far inland of the inundation zone. For example, salt-spray, storm surges, and salt water infiltration up rivers and ditches may double the area affected by rising seas. In particular, regions that feature soils with high or-

ganic content such as the peat-based soils of much of the Albemarle Region are at greater risk because organic soils experience rapid decomposition by sulfate-reducing bacteria in the presence of salt (Hackney and Yelverton 1990). Thus, the large island of dry ground shown northeast of Lake Mattamuskeet in Figure A will not last very long as it is an area of pocosin (sclerophyllous shrub swamp) on a peat dome. The Albemarle Region is highly favored for the conservation of coastal ecosystems. The area's rich mosaic of forests, dunes, wetlands, rivers, and sounds provides an extraordinarily productive natural system. The Albemarle Sound is part of the largest closed lagoon in the world, and part of the second largest and healthiest estuary in the eastern United States. The Roanoke River floodplain contains vast areas of cypress–tupelo swamp forests and the largest and least disturbed bottomland hardwood forest ecosystems remaining in the mid-Atlantic region. Natural fires, floods, and storms are so dominant in this region that the landscape changes very quickly. Rivers routinely change their courses and emerge from their banks. The Outer Banks have been described as a “river of sand” flowing south along the



continental shelf (Kaufman and Pilkey 1983). Xeric environments of sand dunes and ridges share ecotones with the hydric environments of sounds and pocosins. Several national wildlife refuges are located in the region, as are conservation lands established by The Nature Conservancy, the NC Coastal Land Trust, the NC Wildlife Resources Commission, and other private and public agencies. Up to half of the lands at risk from rising seas are conservation lands, established and maintained for the public benefit.

The managers of conservation lands are mainly uncertain about what actions they could take in the face of global climate

change (Lavendel 2003). No one really knows how much or how fast the sea will rise. The responses of public officials (e.g., the U.S. Army Corps of Engineers) are unpredictable, but they tend toward addressing the symptoms of rising seas as temporary, local disasters. The frequency and strength of storms, impacts on precipitation (amount and distribution), and even the responses of plants and animals are not known, and may not be knowable. New species will invade, native species will be stressed, and sometimes native species themselves will become invasive. The only thing that can be predicted with certainty is that the landscapes and seascapes of the Albemarle Region soon will change

dramatically. An engineering or deterministic response—one where the desired future condition is posited against known stresses to determine ideal strategies—is simply impossible. Adaptive management—treating management as a real world, real-time, disciplined, scientific experiment (Holling 1978, 1982; Holling and Meffe 1996) is the only viable alternative.

Ecological stresses can be grouped into three general categories. Some stresses are relatively brief in duration or affect relatively small areas. These stresses (disturbances) modify an ecosystem locally without changing its normal ranges of composition, structure, or function. Other stresses maintain pressure on an ecosystem so that composition, structure, and function change gradually and adaptively. Finally, some stresses are severe enough to cause the ecosystem to change substantially and suddenly, nearly always toward simplification of composition, structure, and function. This kind of change is called a “catastrophe” (Poston and Stewart 1978; Scheffer et al. 2001). Ecological managers must conserve normal disturbance regimes (even as they change) and conserve adaptability to chronic stresses (even as they change). The most important strategy, therefore, is to prevent catastrophic (sudden, simplifying) changes.

The challenge we face in the Albemarle Region of northeast North Carolina can be summarized as follows:

**Uncertainty:** We must accept the overwhelming probability that the sea will continue to rise at an increasing rate; that temperatures will rise; that frequency and severity of storms will probably increase; and the amount, frequency, and duration of precipitation will change unpredictably. Ecosystems and organisms will respond unpredictably in both ecological (within generation) and evolutionary (between generations) time scales.

**Desired outcome:** Ideally, the area in conservation in the Albemarle Region will include both current conserved lands and waters with their future ecosystems, including estuaries and bottoms, and newly conserved lands and waters that seem likely, by virtue of spatial and ecological adjacency, to provide refuge or transitional habitat for ecosystems that are currently conserved.

**Strategy:** We cannot describe confidently the future ecosystems or, given the high probability of both invasion and adaptation, even the future organisms of the Albemarle Region. Even the ecological near future is virtually unknowable. However, we can take steps now—plausible steps based on literature review, modeling, and expert opinion—to reduce the likelihood of catastrophic transformations. We must formulate testable hypotheses about the best ways to mitigate catastrophic change. We must implement these hypotheses in many places, and we must closely monitor each replicate so that we can detect local failures. We must adapt our management as necessary to minimize the likelihood of catastrophic transformation across the region.

**Tactics:** Several management actions are under consideration for immediate application in the Albemarle Region. These tactics group loosely into two groups—conservation and restoration. The conservation tactics involve acquisition and preservation of additional conservation lands, especially inland and upland of existing conservation lands to facilitate the movement of species away from rising seas. Where we suspect vegetation types may move inland or upland, we should actively resist additional fragmentation of the landscape, especially through the construction of new drainage ditches and paved roads; and we must resist the tremendous pressure to armor shores (e.g., with rip-rap, sea walls, bulkheads). An armored shore is only a temporary impediment to the rising sea, while it is a near-permanent impediment to the inland migration of coastal wetlands. We should acquire easements that prevent armoring the shore, especially where it is not already developed (e.g., see Titus 1998).

There are several possible restoration tactics that can be implemented. As the sea rises, drainage ditches that were originally dug to provide farmland and prevent mosquitoes now serve as canals for the intrusion of salt water into areas of peat soils. Installing tide gates and selectively plugging ditches represents an approach to reducing the impacts of salt intrusion and peat soil reduction over much of the non-littoral interior of the region. These ditches are not widely recognized as avenues for salt water intrusion, and they are managed by powerful drainage district associations (Figure B).

Shore lands that are likely to be submerged in the short term can be planted immediately with brackish marsh species, such as brackish needle rush or bald cypress (Figure C). The native bald cypress (*Taxodium distichum*) is tolerant of brackish water, capable of persisting for decades, and even centuries after its roots are submerged by the waters of Albemarle Sound. We should plant bald cypress and perhaps other brackish-tolerant woody species, wherever the land has been cleared. We may be able to subsidize these plantings by offering carbon sequestration credits or timber investment opportunities. We should actively manage standing forests for the restoration of their missing bald cypress component.

The native beds of submerged aquatic vegetation in Albemarle Sound have been severely reduced over the years by human actions (trawling, dredging, sedimentation). We should begin restoration of these beds immediately.

Lastly, as Albemarle Sound inevitably grows more salty and more physically active as the sea rises and the Outer Banks are breached, we should establish and seed marl reefs to provide habitat for native oysters (Figure D) to maintain water quality in the sounds and to buffer the fragile, newly submerged shore from physical erosion.



**Figure B** Thick peat deposits on the Albemarle Peninsula are vulnerable to salt water intrusion due to sea level rise. Numerous ditches throughout the region can bring rising sea water further inland, where the thickest peat deposits can be destroyed. (Modified from Poulter 2005.)

(I)



(II)



**Figure C** Examples of vegetation adapted to brackish and submerged conditions that can be planted in anticipation of sea level rises. (I) Brackish needle-rush marsh invading dry land due to current sea level rise. (II) A bald cypress swamp (*Taxodium distichum*) in North Carolina. (I, photograph by Sam Pearsall; II, photograph © Gary Retherford/Photo Researchers, Inc.)

## Conclusions

In the Albemarle Region, the proportion of lands likely to be affected by rising seas is very high—among the highest in the world. And the proportion of those endangered lands in public ownership and conservation management is also very high. Local ecosystems and species are highly adaptable, and although the nature of the adaptations are not predictable, this is a region where manipulating the placement of species possess-

ing adaptations to rising sea levels have a good chance of avoiding catastrophic transformations. We have a list of practical management actions to try, so that adaptations over an ecosystem level have time to happen. We have professional conservation managers in place, and we have the instrument of adaptive management to stave off failure and increase the probability of success. We must begin implementation immediately, and we must continue as long as the sea continues to rise.

(I)



(II)



**Figure D** (I) Building oyster reefs with marl. (II) Building oyster reefs with empty oyster shells. (I, photograph by Ashley Harraman Burgin; II, photograph courtesy of NOAA.)

## CASE STUDY 10.4

### Climate Change and Coastal Migrant Birds

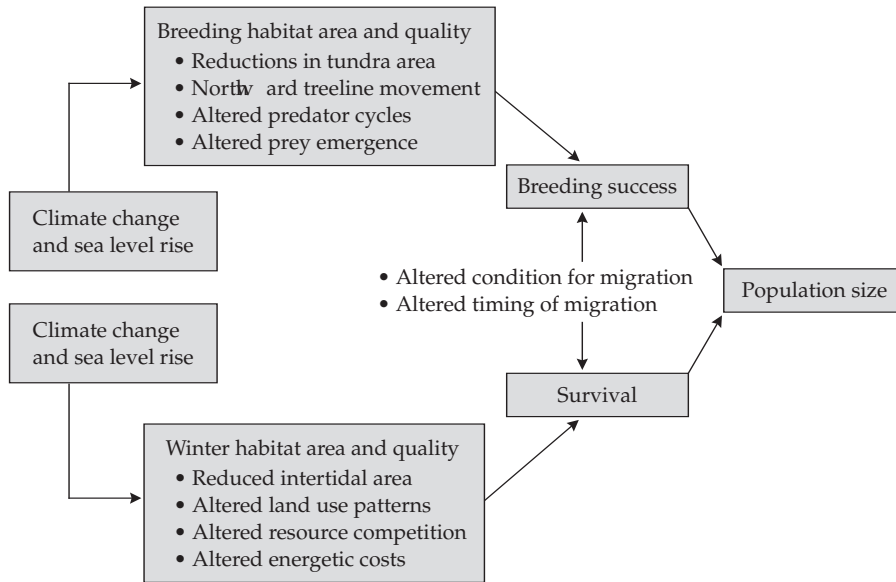
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Coastlines around the world are in a time of rapid change as a consequence of rises in global sea levels combined with extensive human development and exploitation. Coastal zones also harbor some of the habitats with greatest biological diversity and economic importance. The implications of these changes are thus potentially severe, and our ability to manage coastlines to minimize these impacts will rest on our ability to predict the consequences of coastal change, in order to guide effective management policies.

Among the groups most reliant upon coastal zones are migratory birds that breed in Arctic and subarctic regions, but depend upon highly productive temperate coastal mudflats to survive the winter and fuel their journeys to and from the Arctic. Climate change may deal a double blow to these species, as both Arctic regions and temperate coastal zones are likely to change substantially in response to global warming and sea level rise (Watkinson et al. 2004). Arctic zones are extremely vulnerable to

increases in glacial and icecap melt altering the duration of freeze and thaw periods, and to northward movements of tree-lines as climatic suitability for forests increases at higher latitudes (Weller and Lange 1999; IPCC 2001b; Bigelow et al. 2003). Declines in the area, and potentially also the suitability, of arctic and subarctic habitats are likely to have serious consequences for the millions of migratory birds that breed in these areas. At the opposite end of the migratory range, coastal mudflats in temperate and tropical zones are threatened both by a reduction in area, as hard coastal defenses prevent the natural inland migration of coastal habitats, and by the extensive human developments that frequently replace these key habitats, together with human exploitation of the resources within them.

Figure A describes some of the main ways in which climate-induced changes to breeding or wintering habitat may influence population size in coastal migrant birds, through direct or indirect impacts on demographic processes. Large-scale



**Figure A** Examples of the mechanisms by which climate change and sea level rise are likely to influence population size in migratory birds that breed in the Arctic and overwinter in temperate coastal zones.

changes to habitat structure clearly have the potential to influence population size dramatically in many of these species, through processes such as limiting the availability of breeding locations or foraging sites and hence increasing competition for the remaining resources. Models of vegetation change suggest that many arctic breeding bird species may experience losses of over 50% of current breeding habitat (Zöckler and Lyсенko 2000). However, in some cases the less obvious effects (e.g., changes in predation levels or energetic costs) may also be important. Many high-arctic migrants face huge energetic costs in traveling to and from the breeding grounds each year, in some cases requiring dramatic annual physiological changes (Piersma 1998; Battley et al. 2000). This energetic expenditure needs to be fuelled by the continued availability of food resources along a network of wintering and passage sites. Similarly, many predator species at high latitudes undergo population cycles that result in cyclic levels of predation on migratory birds (e.g., Bety et al. 2002). Changes in predator abundance or the timing of the breeding season could potentially lead to a decoupling of these cycles, with unknown consequences for either party. Ultimately the influence of any of these changes on population size will depend on the density-dependent nature of each of the processes, which is frequently the most difficult aspect to quantify (Sutherland 1996).

While the loss of tundra habitat is very likely to have serious negative consequences for breeding birds, impacts of climate change at passage and wintering sites at lower latitudes are less easy to predict. In many areas, sea level rise and the presence of hard sea defenses may result in reductions in intertidal areas through coastal squeeze, with likely serious impacts on the

species present. However, in response to these processes, wetland restoration is taking place in some coastal areas and, in the U.K., managed realignment of sea defenses is being undertaken at a growing number of sites (Perrow and Davy 2002; Pethick 2002). These habitat creation initiatives could therefore result in net benefits for some species (e.g. Evans et al. 1998). However, the loss of vulnerable low-lying coastal wetlands adjacent to intertidal areas may be more difficult to mitigate. Species dependent on these habitats, or on the juxtaposition of intertidal and coastal freshwater habitats, may be the ones most likely to suffer if these habitats cannot be protected or recreated.

Environmental changes at one end of the migratory range can also have consequences elsewhere in the range. For example, seasonal declines in productivity mean that individual migrants are under strong selective pressure to return to the breeding grounds as soon as possible (Kokko 1999; Drent et al. 2003). The timing and abundance of resources on spring passage sites prior to departure for the Arctic can therefore be critical in facilitating these rapid departures (e.g., Prop et al. 2003 and Battley et al. 2004). The productivity and abundance of many intertidal invertebrates that form a key part of these resources can be strongly temperature-dependent (Beukema et al. 1996; Honkoop and Beukema 1997). Hence, changes in prey abundance through habitat change and temperature shifts are likely to influence the timing of arrival of migrants in the Arctic and the condition that they arrive in. The short window of time in which prey are available in the Arctic also magnifies the importance of the breeding period coinciding with peaks in prey abundance. Any change in spring conditions on passage sites or in the Arctic could potentially result in a mismatch between arrival time and the availability of breeding sites and prey supplies. The impact of any such mismatches will depend on the cues used by migrants to time their departures and arrivals, and their ability to adapt their migratory schedule to changing environmental conditions.

Predicting the impact of climate change and sea level rise on migratory birds therefore requires an understanding of the processes that influence population size in both the breeding and the wintering grounds, and any interactions between them. In particular, the density-dependent processes that regulate population size need to be quantified over these very large spatial scales. An example of the interactive nature of population size, distribution and demography is provided by the Black-tailed Godwit, *Limosa limosa islandica*, a migratory



**Figure B** Many shorebird species are particularly vulnerable to sea level changes due to climate change, such as this Black-tailed Godwit (*Limosa limosa islandica*). (Photograph © Bernard Castelein/naturepl.com.)

shorebird that breeds in Iceland and winters in temperate western Europe (Figure B). This species provides an ideal opportunity for studies of large-scale population processes because recent rapid population increases have resulted in a change in spatial distribution across U.K. wintering sites that follows a clear buffer effect; in the 1970s the population was originally concentrated in good-quality winter sites in the south of England, where rates of prey consumption are high, but since then it has expanded into poorer-quality sites in the east of England where prey intake rates are lower (Gill et al. 2001).

The establishment of a network of volunteer observers right across the range of the Icelandic Black-tailed Godwit has resulted in thousands of records of individually color-marked birds over several years. This has allowed direct comparisons of survival rates of birds wintering in traditionally and recently occupied wintering sites. The between-site differences in prey consumption rates are mirrored by differences in annual survival; birds wintering in the high-quality, traditionally occupied sites have significantly higher survival rates than those in the recently occupied, poorer-quality sites (Gill et al. 2001).

The question of whether the quality of winter habitat might affect breeding performance was then assessed by measuring the timing of arrival of individual birds in Iceland. These data demonstrated that individuals from higher-quality winter locations arrived significantly earlier than those from poorer-quality

locations (Gill et al. 2001). Thus winter habitat quality not only affects survival rates in Black-tailed Godwits, but also influences timing of arrival on the breeding grounds, which is likely to confer an advantage in breeding success. Population expansion into poorer-quality locations therefore appears to have the potential to influence population size through the impact on per capita survival, and on delayed arrival on the breeding grounds.

These interactions suggest that the impact of climate change on the Black-tailed Godwit population will vary depending on which habitats and locations are subject to the greatest change. As individuals inhabiting good-quality wintering sites experience higher survival and return to the breeding grounds earlier, the loss of good-quality habitat is likely to have a disproportionate effect on population demography. By contrast, the loss of poor-quality habitat may have a relatively minor impact on population size. This provides scope for both targeted conservation efforts to both protect higher-quality sites and improve habitat quality as a form of mitigation.

While reducing the impacts of climate change in Arctic zones will require global policy responses to reduce carbon emissions, the impacts on temperate coastal zones can also be addressed to a large extent through appropriate management to reduce the human pressures on these valuable habitats. In theory, such management approaches are simple: prevent any developments that threaten the integrity of the habitat, restrict all human exploitation of the resources within the habitat, and begin a program of removing sea defenses to allow the habitats to move inland in response to sea level rise. In practice, of course, there are many constraints on these policy options and coastal managers must make key decisions about which areas of land need to be afforded different types of protection. What is required of conservation biologists therefore is to inform these decision-making processes, ideally through the development of predictive models to assess the consequences of different coastal management options. Such models require integrated, interdisciplinary approaches to science to effectively link the climatological, oceanographic, geomorphological, and ecological processes that need to be incorporated. This is a tall order, but one that research groups, such as the Tyndall Centre for Climate Change Research, are beginning to tackle. The science relating to each of these processes has been developed largely in isolation, and each has significant uncertainty yet to be unraveled. Nevertheless, decisions will be made whether or not conservation biologists are prepared to attempt to influence these processes.

Coastal zone managers across the globe are being faced with serious decisions regarding future management strategies in response to climate change and sea level rise. The challenge for conservation biologists is both to improve our understanding of the processes influencing population regulation in many more species, and to better direct our findings toward policymakers so that effective conservation forms a cornerstone of these decision-making processes.

## Summary

1. The greenhouse effect is nothing new. The presence of greenhouse gases, such as carbon dioxide, in Earth's atmosphere allow heat to be retained at the surface, making the world about 60°F warmer than it would be without the greenhouse effect. Our use of fossil fuels (oil, coal, and natural gas) is releasing large amounts of carbon that have been stored deep underground for many millions of years. Levels of carbon dioxide in the atmosphere are 30% higher than before the Industrial Age, and this percentage increases every year. This has enhanced the greenhouse effect, causing the surface of Earth to gradually become warmer. In 2001, the Intergovernmental Panel on Climate Change concluded that the global rise in average yearly temperature over the past 50 years was due primarily to increased concentrations of anthropogenic greenhouse gases. Because carbon dioxide is very stable, and combustion of fossil fuels continues, global warming trends are expected to continue, with large impacts on local and regional climate patterns. Current and future human-induced changes in the global climate will directly affect regional conditions, such as geographic patterns of temperature and precipitation.
2. Biologists and paleontologists have spent the past 150 years documenting the crucial role of climate in determining the geographical distribution of species and ecological communities. Climate variability and change can affect plants and animals in a number of ways, including their distributions, population sizes, and even physical structure, metabolism, and behavior. The timing of important ecological events, including the flowering of plants and the breeding times of animals also shifts in conjunction with climate change.
3. Recent analyses at both the global level and at the scale of the U.S. have estimated that more than half of all wild species have shown a response to twentieth century climate change. For many species, biologists understand the underlying mechanisms driving a species' sensitivity to particular temperature or precipitation thresholds.

Geographic ranges for some plants and animals have shifted northward and upward in elevation, and in some cases, contracted. Range shifts have been observed in organisms as diverse as birds, mammals, intertidal invertebrates, and plants. Such major shifts in species' locations alter species composition within communities, and thus species interactions. In particular, such shifts in composition are likely to alter important competitive and preda-

tor-prey relationships, which can reduce local or regional biodiversity.

4. Ecosystem processes such as carbon cycling and storage have been altered by climate change. The lengthening of the growing season has altered the annual cycle of carbon dioxide (CO<sub>2</sub>) levels in the atmosphere, because plants are a major intermediary for carbon flow through ecosystems, with changes in carbon storage and release patterns. Climate change has the potential to degrade ecosystem functions vital to global health.

The findings that climate change is affecting biological systems are consistent across different geographic scales and a variety of species. Even against a background of apparently dominating forces such as direct human-driven habitat destruction and alteration, a climate "fingerprint" is discernible in natural systems.

5. Future biological consequences of anthropogenic climate change are more likely to include range contractions than range shifts. During historic glacial cycles, range shifts of hundreds to thousands of miles were common, and species extinction was rare. However, achieving such massive relocation is much less likely across the human-dominated, artificially fragmented landscapes of today. Species that are not adapted to urban and agricultural environments are likely to be confined to smaller total geographic areas as climate causes them to contract from their southern and lower boundaries. Already rare or endangered species, or those living only on high mountaintops, are believed to have the highest risk of extinction.
6. Reducing the adverse effects of climate change on ecosystems can be facilitated through a broad range of strategies, including adaptive management, promotion of transitional habitat in nonpreserved areas, and the alleviation of nonclimate stressors. The protection of transitional habitat that links natural areas might assist in enabling species migration in response to climate change. Meanwhile, promoting dynamic design and management plans for nature reserves may enable managers to facilitate the adjustment of wild species to changing climate conditions (e.g., through active relocation programs). Also, because climate change may be particularly dangerous to natural systems when superimposed on already existing stressors, alleviation of the stress due to these other anthropogenic factors may help reduce their combined effects with climate change.
7. The international community has responded to the threats of climate change by developing agreements

for reductions in greenhouse gas emissions. The most prominent of these is the Kyoto Protocol, which is likely to become international law by the end of 2005. Within the U.S., individual cities and states have fostered incentives for “green” energy programs (e.g., wind and solar), with the result that local electricity is often from a mix of traditional fossil-fuel burning plants and emission-free sources. Policies committed to reducing greenhouse gas emissions cannot stop climate change, but they can have a large influence on minimizing the magnitude and rate of change over the next 100 years. Keeping climate change to a minimum is vital to allow both wild species and human managers to adapt to a dynamically changing environment.

Please refer to the website [www.sinauer.com/groom](http://www.sinauer.com/groom) for Suggested Readings, Web links, additional questions, and supplementary resources.

## Questions for Discussion

1. What trends have been documented in twentieth century global and U.S. climate?
2. Why are certain gases called “greenhouse” gases and where do they come from? Which gas is the main one being focused on in policy and why is it increasing?
3. What are the main lines of evidence that wild species, in general, have been affected by twentieth century global climate change? How do we know these changes aren’t just natural, or due to the many other things humans are doing?
4. How does twentieth century climate change compare to past major (natural) climate changes? What is different about the modern world that makes climate change more likely to cause harm now (and hence be a conservation problem) than it did in the geological past (e.g., over the several hundred thousands of years of glacial–interglacial cycles)?
5. What recommendations would you give to conservation groups to help them reduce loss of biodiversity under climate change? What would you do if you were the manager of a reserve? What would you consider in designing and buying new reserves to make the species they are protecting more resilient to climate change?