GREENHOUSE EFFECT

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GLOSSARY

aerosols Microscopic airborne particles.
albedo The fraction of light hitting a surface that is reflected.
anthropogenic Resulting from human activities.
climate sensitivity Long-term change in global mean surface temperature following a doubling of equivalent carbon dioxide (CO₂) concentration in the atmosphere.
Earth energy balance Average balancing of incoming solar energy by outgoing terrestrial radiation for Earth as a whole.
equivalent CO₂ concentration Concentration of carbon dioxide that would cause the same amount of radiative forcing as a mixture of carbon dioxide and other greenhouse gases.
feedback Change in a system component that triggers effects that eventually change the original component again. Feedbacks can be positive (self-reinforcing) or negative (self-dampening).
greenhouse gases Atmospheric gases that can absorb and reradiate infrared radiation.
radiative forcing Measure used to express and compare the potential of climate change factors to perturb the Earth energy balance, reported in watts per square meter (W m⁻²). A positive radiative forcing tends to warm the Earth’s surface and a negative radiative forcing tends to cool the surface.

THE “GREENHOUSE EFFECT” REFERS TO THE PROCESS by which infrared radiation-absorbing gases in Earth’s atmosphere trap heat and thus influence climate. This article gives an overview of the anthropogenic loading of greenhouse gases into the atmosphere and associated effects on recent and future climate change, summarizes feedback effects, and describes potential and current impacts of climate change on biodiversity.

I. INTRODUCTION

Earth’s climate, from daily weather events to glacial and interglacial cycles, is driven by the amount of radiation received from the sun and how that radiation is distributed throughout the global Earth–atmosphere system. The atmospheric greenhouse effect acts as an important factor in establishing a temperature that is hospitable for life. The basic mechanism is simple and was first
detailed by the Swedish physicist Svante August Arrhenius in 1896. Light from the sun largely penetrates the atmosphere and is absorbed at the planetary surface. There, it is converted from energy in the form of light to energy in the form of heat (longwave infrared radiation). As the surface temperature rises because of this heat, Earth radiates more and more heat back out to space, thereby maintaining an energy balance. Several gases in the atmosphere, referred to as "greenhouse gases," absorb some of the heat emitted from Earth's surface and reradiate it back toward the surface, causing the temperature to rise. Without this naturally occurring greenhouse effect, Earth's average surface temperature would be ~19°C, about 33°C colder than it is today. The term "greenhouse effect," though popular, is a misnomer because the warming effect of glass greenhouses is due primarily to suppression of convection, not trapping of infrared radiation.

II. ENHANCED GREENHOUSE EFFECT

The most important naturally occurring greenhouse gases are water vapor, carbon dioxide (CO₂), methane (CH₄), nitrous oxide (N₂O), and ozone (O₃). Although water vapor plays the biggest role in generating the natural greenhouse effect, anthropogenic emission of the other gases, along with artificially produced chlorofluorocarbons (CFCs), are most important in generating an enhanced greenhouse effect. Detailed instrument data show that concentrations of these gases have been increasing since preindustrial times (~1750) (Table I), particularly in recent decades, largely due to human industrial, agricultural, and urbanization activities. As the concentrations of greenhouse gases increase in the atmosphere, they continue to trap and reradiate more and more heat, resulting in rising surface temperature and other climatic changes.

Increases in CO₂ account for about 65% of the current direct positive radiative forcing due to anthropogenic loading of greenhouse gases (Fig. 1). The atmospheric CO₂ concentration has increased 30% since preindustrial times, as a result of increasing emissions from fossil fuel combustion, land conversion, and cement production, and is continuing to increase by 0.4% per year (Fig. 2). If future emissions of CO₂ are maintained at 1994 levels, its atmospheric concentration will be close to double the preindustrial level by the end of the twenty-first century. In the absence of strong emissions controls, given increasing global energy and resource consumption, CO₂ concentrations may double by 2040 and will continue to increase dramatically (Fig. 3). Concentrations of other greenhouse gases, particularly methane and nitrous oxide, are also expected to rise, resulting in an earlier doubling of the equivalent CO₂ concentration. Greenhouse gases tend to remain in the atmosphere for many years (see Table I) and consequently are well mixed. They continue to affect the climate long after initial emissions and later stabilization of atmospheric concentrations.

Aerosols can alter the climate by changing atmospheric albedo. These fine particles absorb and reflect solar radiation and alter cloud properties. Sulfate aerosols from fossil fuel emissions and smelting tend to have a negative effect on radiative forcing and thus cool the climate. Current estimates of direct radiative forcing are −0.5 W m⁻² due to aerosols compared to 2.45 W m⁻² due to greenhouse gases (see Fig. 1). Unlike greenhouse gases, aerosols are very short-lived in the atmosphere and therefore are not well mixed and respond rapidly to changes in emissions.

III. CLIMATIC CONSEQUENCES: GLOBAL WARMING

A. Past Climate Change

Scientists use deep ice cores drilled from glaciers in Antarctica, Greenland, and South America to examine ancient climate and atmospheric trends over the last several hundred thousand years. The data from these ice cores reveal a strong correlation between temperature and CO₂ concentrations (see Fig. 3) and suggest that a doubling of CO₂ has been historically associated with a 3 to 4°C temperature increase (Lorius et al., 1990). However, it is uncertain whether (1) the observed increases in CO₂ drove the warming or whether (2) warming due to planetary orbital changes drove increases in CO₂. If the first hypothesis is correct, the historic temperature sensitivity to natural CO₂ increases is comparable to that expected from anthropogenic loading of greenhouse gases (see Section III,C). If the second hypothesis is correct, current climate models may underestimate how much temperature will increase in response to anthropogenic additions of greenhouse gases to the atmosphere. If an initial warming (whether from orbital changes, greenhouse gases, or some other factor) results in more atmospheric CO₂ and other greenhouse gases, the increased gases would tend to drive additional warming. This would represent a positive feedback effect that is currently not included in climate models (see Section IV).
TABLE I
A Sample of Greenhouse Gases Affected by Human Activities

<table>
<thead>
<tr>
<th></th>
<th>CO₂</th>
<th>CH₄</th>
<th>N₂O</th>
<th>CFC-11</th>
<th>HCFC-22</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-industrial</td>
<td>~280</td>
<td>~700</td>
<td>~275</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>concentration</td>
<td>ppmv</td>
<td>ppbv</td>
<td>ppbv</td>
<td>ppbv</td>
<td>ppbv</td>
</tr>
<tr>
<td>1994 concentration</td>
<td>358</td>
<td>1720</td>
<td>312</td>
<td>268</td>
<td>110</td>
</tr>
<tr>
<td>Rate of change</td>
<td>1.5</td>
<td>10</td>
<td>0.8</td>
<td>0</td>
<td>1.2</td>
</tr>
<tr>
<td>% rate of change</td>
<td>0.4%</td>
<td>0.6%</td>
<td>0.25%</td>
<td>0.6%</td>
<td>5%</td>
</tr>
<tr>
<td>Atmospheric</td>
<td>50–200</td>
<td>12</td>
<td>120</td>
<td>50</td>
<td>12</td>
</tr>
<tr>
<td>lifetime (years)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Direct radiative</td>
<td>1.56</td>
<td>0.47</td>
<td>0.14</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>forcing (Wm⁻²)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Adapted from Houghton et al. (1996) by permission from the Secretary of the IPCC.
  ppmv, parts per million by volume; ppbv, parts per billion by volume; pptv, parts per trillion by volume.
  No single lifetime for CO₂ can be defined because of different rates of uptake by different sink processes.
  This has been defined as an adjustment time which takes into account the indirect effect of methane on its own lifetime.
  This is the direct radiative forcing due to CFCs and HCFCs combined. However, their net radiative forcing is reduced by about 0.1 Wm⁻² because they have caused stratospheric ozone depletion which gives rise to a negative radiative forcing.
  The growth rates of CO₂, CH₄, and N₂O are averaged over the decade beginning 1984; halocarbon growth rates are based on 1990–1994 data.

B. Recent Climate Change

Recent observational data not only document increased atmospheric concentrations of greenhouse gases, but also reveal the first “fingerprint” of human-induced global warming. Global average surface temperature trends reveal a 0.3 to 0.6°C temperature increase during the twentieth century, with the ten hottest years on instrument record occurring after 1980. Models that take into account both the positive effects of greenhouse gases and the negative effects of aerosols predict the observed upward trend of temperature quite closely (Fig. 4), including perturbations like the temporary decrease in global average temperature due to stratospheric aerosol loading from the 1991 Mt. Pinatubo volcano eruption. The current consensus among scientists is that “the balance of evidence suggests a discernible human influence on global climate” (Houghton et al., 1996) (see Box 1).

How do the recent temperature increases compare to natural climate variability? The long-term climatic record is quite variable, with changes of up to 1°C per decade during the most volatile periods of transition from the last glacial to the current interglacial period. However, in the last 10,000 years of the current interglacial period, fluctuations have generally not exceeded 1°C per century, making it unlikely that the recent observed trends and expected increases in temperature over the next 100 years are merely due to natural climate variability.

C. Future Climate Change

What will the future bring? General circulation models (GCMs) integrate the physics of radiative forcing, ocean dynamics, and other complex Earth–atmosphere processes in order to simulate and predict climate trends. The current consensus, based on multiple GCM forecasts, is that a doubling of equivalent CO₂ concentration (referred to as “2 × CO₂”) in the atmosphere over preindustrial concentrations will result in a global mean average temperature increase of 1 to 3.5°C (Houghton et al., 1996). A 2 × CO₂ atmosphere is used as a benchmark by climate change scientists to establish climate sensitivity and to compare scenarios and predictions, but greenhouse gas concentrations will continue to increase beyond a doubling, resulting in even greater temperature increases.

GCM and associated simulation studies point to many climatic impacts of increases in greenhouse gases and aerosols that will be of particular importance to ecosystems and biodiversity. First, surface warming will
not be uniform. Under a $2 \times CO_2$ atmosphere, average temperature increases are predicted to be greatest at the poles ($\approx 10^\circ C$) and least at the equator ($\approx 1^\circ C$). Winter temperatures will increase more than summer temperatures, and nighttime more than daytime temperatures. The incidence of record-breaking hot days will tend to increase in the summer, and fewer frost days are likely to occur in the winter. Second, warming is predicted to increase evaporation and global mean precipitation, and may increase cloud cover. High and middle latitudes and elevations are predicted to experience increases in winter precipitation, more winter precipitation falling as rain, earlier snowmelt, and reductions of summer soil moisture in noncoastal areas. Tropical precipitation is likely to change, but how it will change is uncertain. Third, the frequency and intensity of extreme weather and disturbance events (e.g., drought, deluge, summer heat waves, hurricanes, fires) are expected to increase. Fourth, glaciers are predicted to retreat and melt, sea levels may rise up to 95 cm as a result of a $2 \times CO_2$ atmosphere, and surface waters are likely to warm.

Some of these trends have already been observed in recent climate data. For example, more warming has occurred toward the poles, nighttime temperatures have increased more than daytime temperatures, warming has been greatest over the midlatitude continents in winter and spring, snowpack is decreasing and snowmelt is occurring earlier at high latitudes and elevations, glaciers are retreating, and sea levels have risen 10–25 cm during the last 100 years.

IV. FEEDBACKS

A. Geophysical Feedbacks

Recent general circulation models include not only mechanisms underlying direct greenhouse gas and aerosol radiative forcing, but also mechanisms underlying three large feedback processes: water vapor, snow/ice albedo, and cloud cover. Because the capacity of the atmosphere to hold water vapor increases as it warms, and because water vapor acts as a greenhouse gas to
FIGURE 2  CO₂ concentrations over the past 1000 years from four Antarctic ice core records (D47, D57, Siple, and South Pole) and since 1958 from the Mauna Loa, Hawaii, measurement site. The solid curve is based on a 100-year running mean. The inset curve shows fossil fuel CO₂ emissions since 1850. (Reprinted from Houghton et al., 1996, by permission from the Secretary of the IPCC.)

further increase temperature, a positive feedback to the climate is created that amplifies warming. The snow/ice albedo effect is also a positive feedback—as warmer temperatures melt highly reflective snow and ice at the poles and high elevations, thus lowering surface albedo, Earth will absorb and radiate more infrared radiation, which will augment warming. Cloud formation adds much of the uncertainty to GCM estimates because the impacts of warming and other changes to the atmosphere on cloud formation are myriad and difficult to predict. In addition, because clouds can form at many heights, over land or water surfaces with differing albedos, and with many shapes, clouds can have multiple negative and positive feedback effects.

B. Biogeochemical Feedbacks

As complex as GCMs are, they fail to incorporate many potentially important aspects of chemical and ecological processes that are likely to produce additional feedback effects. Though it is likely that none of these feedbacks is individually as strong as the geophysical feedbacks already incorporated into GCMs, together they represent a potentially significant perturbation to the climate system. Biogeochemical feedbacks could greatly increase climate sensitivity to a 2 × CO₂ atmosphere (up to 8–10°C; Lashof, 1989) compared to current model predictions (1–3.5°C). Many biogeochemical feedbacks due to global warming will also interact with other anthropogenic stresses, such as deforestation and pollution, to further exacerbate or reduce climate change effects at local, regional, and global scales.

1. Marine Feedbacks

Global warming is likely to drive many complex marine-based feedback processes, of which only a few are mentioned here. With regard to geochemistry, the warming of ocean surface waters expected under climate change will reduce the capacity of those waters to hold dissolved CO₂, resulting in a positive feedback since less CO₂ will be removed from the atmosphere. If the additional surface water warmth travels down the water column, methane could be released from temperature- and pressure-sensitive hydrates that are present in some ocean floor sediments. This would also result in a positive feedback since the released methane, a greenhouse gas, would cause more warming.

With regard to biology, more than a third of annual global primary production occurs in ocean surface waters, primarily by microscopic single-celled organisms
Box 1

Critical Viewpoints and Responses

Although scientists currently have reached a strong consensus regarding the relationship between atmospheric loading of greenhouse gases and recent and projected global warming trends, a few critics express alternative viewpoints about climate change. Responses to some skeptical views follow:

1. The global warming trend over the past 100 years is the result of an increasingly brighter sun. No mechanism is known that could convert the observed very slight changes in solar output into a warming trend consistent with observations.

2. Satellite data disprove the hypothesis that recent warming is due to greenhouse gases. Satellite data cover too short of a period to disprove climate models, but the available satellite data (mostly on upper atmosphere temperatures) are reasonably consistent with model projections.

3. Most of the recent warming occurred earlier in the century but the atmosphere has only dramatically changed more recently. The warming trend since 1970 has been even more dramatic than that early in the century, consistent with the increasing rate of atmospheric greenhouse gas buildup.

4. A cooling trend during the period 1940–1970 contradicts our climate models. The observed cooling trend resulted from measured increasing levels of aerosols and dust in the atmosphere during that period. Although climate modelers initially failed to include atmospheric particulates in their analyses, when particles are included, the model predictions are consistent with observation.

5. We will welcome global warming because an ice age is coming. The timescale at which Earth will cool is over several thousand years and will not be counteracted by anthropogenic climate change. Over millennia, the current anthropogenic warming episode will slowly dissipate as humans stop loading greenhouse gases into the atmosphere and as most of the excess CO₂ is naturally sequestered in the deep oceans.
called phytoplankton, which form the base of the oceanic food web. Through the process of photosynthesis, CO$_2$ is fixed by the phytoplankton and thus transferred from the atmosphere to ocean surface waters. Some of that fixed carbon, in the form of dead bodies and fecal matter of phytoplankton and other organisms, sinks into deep ocean layers and sediments and is sequestered there, where it can no longer be exchanged with the atmosphere on short timescales. This process is referred to as the "biological carbon pump" and has been important in maintaining a level of CO$_2$ in the atmosphere that is currently about 40% lower than it would be in the absence of marine organisms. Because the amount of marine primary production is dependent on the supply of nutrients and sunlight to ocean surface layers, any way in which global warming alters those inputs can create feedbacks to warming. One of many hypothesized feedbacks, in this case positive, is that global warming will tend to diminish the intensity of the oceanic circulation of nutrients, leading to more homogeneous, diffuse ocean productivity and hence a decrease in the amount of carbon "pumped" into deep ocean layers (Rowe and Baldas, in Woodwell and Mackenzie, 1995).

2. Terrestrial Feedbacks

About three times as much carbon is stored in terrestrial vegetation and soils than is stored in the atmosphere. Through photosynthesis and respiration, more than one-eighth of atmospheric CO$_2$ is exchanged each year with terrestrial ecosystems. Changes to terrestrial-atmospheric carbon cycling thus have the potential to produce significant feedbacks to climate change. The feedback pathways for carbon in terrestrial ecosystems are complex, representing both positive and negative feedbacks. Perhaps the most well-known potential carbon cycle feedback is the "CO$_2$ fertilization effect," which refers to the stimulation of photosynthesis by increased levels of CO$_2$, which in turn can result in increased plant growth and greater storage of carbon in vegetation. This represents a negative feedback to global warming. However, ecosystem-level experiments appear to indicate that fertilization effects may tend to disappear after a few years, and the magnitude of effects may be strongly impacted by water and nutrient availability (Lashof et al., 1997).

Climatic changes that will accompany higher concentrations of CO$_2$ make it even more complicated to predict the net effect of global warming on the storage of carbon in vegetation and soil versus the atmosphere. For example, under global warming, changes in water availability and temperature will reduce the CO$_2$ uptake and growth of some plants while favoring others. Resulting changes in plant community composition can alter the quantity and quality of litter that enters the soil, which can lead to changes in soil carbon storage. Soil microorganisms will not only respond to changes in litter inputs, but will also be directly affected by changes in climate. Microbes and fungi tend to respire more CO$_2$ to the atmosphere as temperatures increase. However, rates of respiration depend on levels of soil moisture, and different extremes of water availability (both too much and too little) will tend to decrease respiration. The effects of climate change on microorganisms will also alter fluxes of other greenhouse gases such as methane in wetlands (e.g., northern peatlands, which store large amounts of carbon and may be a source of strong positive feedback to warming) and nitrous oxide in moist tropical soils.

In addition to the more direct effects of changes in temperature and moisture on the terrestrial carbon cycle, indirect effects such as the alteration of fire regimes due to climate change may produce significant feedbacks. In general, predicted increases in fire frequency for many ecosystems as a result of global warming may alter the structure of plant communities and result in reductions of terrestrial carbon storage, a positive feedback.

Another set of global warming feedbacks related to changes in albedo may result from climate-induced shifts in land cover and vegetation. The drying of soils and increased desertification expected from global warming will add dust to the atmosphere that, like aerosols, can reduce warming through increases in atmospheric albedo. Surface albedo is also expected to change as the boundaries of biomes shift, since different vegetation types can have different reflectivity. For example, the predicted northward expansion of boreal forest into tundra could decrease surface albedo, resulting in increased surface warming. This mechanism may have acted as a strong positive feedback 6000 years ago when an initial warming at high latitudes as a result of orbital variations appears to have doubled in magnitude owing to changes in surface albedo from boreal forest expansion (Foley et al., 1994).

V. CLIMATE CHANGE AND BIODIVERSITY

A. Introduction

Currently, the largest reductions in biodiversity result from massive deforestation in the tropics, in conjunc-
tion with other sources of worldwide habitat destruction. Even as the raising of vast tracts of tropical forests leads to immediate direct losses of hundreds to many thousands of species per year, the carbon that is released to the atmosphere through deforestation is amplifying the anthropogenic greenhouse effect. Global warming could lead to losses in biodiversity over the next several hundred years that are similar to or greater in magnitude than losses from direct habitat destruction. Dramatic changes in global climate have the potential to disrupt every ecosystem on Earth, leading to a pervasive trend of biodiversity loss due to climate-related habitat alteration, reorganization, and destruction.

Why does anthropogenic climate change present such a threat to biodiversity? There are two main reasons. First, the rate and magnitude of climate change expected over the next several decades to centuries are greater than any changes that current organisms have experienced. Over the last 18,000 years, starting during the last full glacial period and continuing through the current interglacial period that began about 10,000 years ago, average global surface temperature has gradually increased by about 5 ± 1°C (T. Webb, in Peters and Lovejoy, 1992). If we assume conservatively that global warming will increase mean temperature by 5°C over the next 200 years, this represents a 90-fold increase over the recent natural rate of change. In terms of magnitude, a 3°C increase would result in the warmest world in 40 million or more years. Second, global warming will interact synergistically with other anthropogenic stresses such as habitat destruction, pollution, ozone depletion, and alien species introduction to reduce biodiversity by more than just the sum of losses that would occur if each factor occurred independently.

Scientists' ability to specifically predict how biodiversity will be affected by climate change is constrained by large uncertainties associated with local and regional climate change predictions. Much of the following discussion is based not so much on how scientists specifically think biodiversity will change under global warming, but on generic ways in which biota will be affected by global warming that can lead to changes in biodiversity. The term "biota" is used as shorthand to refer collectively to individual organisms, groups of the same types of organisms (populations, species, functional types), and ecological complexes of multiple populations and species (communities, ecosystems). This section summarizes how scientists study the effects of climate change on biota, the types of responses biota can have to climate change, the kinds of biota likely to be harmed by and to benefit from climate change, and evidence for biotic responses to current anthropogenic climate change.

B. How Scientists Study the Effects of Climate Change on Biota

1. Models

Climate-vegetation classification systems are types of static models that are based on the hypothesis that climate patterns are the primary determinant of the broad-scale distribution of vegetation types. In 1947, L. Holdridge developed a "life-zone" concept that used three variables based on temperature and precipitation to predict under what climates 20 vegetation types should occur. Later researchers refined and added detail to this basic concept by using a wider variety of vegetation types and bioclimatic variables that explicitly incorporate drought stress and seasonality (Table II). These types of static models can be compared to current vegetation and climate maps to determine their accuracy and then used in conjunction with maps of simulated future climate to predict shifts in distribution of vegetation types due to global warming. The Holdridge life-zone classification has been used to predict the conversion of much of today's boreal forest into temperate deciduous forest (Emanuel et al., 1985). While classification systems provide ways to look at potential global-scale impacts of climate change on vegetation, they are limited by the fact that climate will change continuously and with considerable interannual variation, rather than shifting abruptly to a new plateau. In addition, many other factors besides climate can influence the movement and distribution of biota, and this greatly reduces the potential accuracy of such models.

### TABLE II

| Bioclimatic Variables Used by E. O. Box to Predict Distribution Limits of Plant Types* |
|----------------------------------|----------------------------------|
| $T_{max}$ | Mean temperature of the warmest month (°C) |
| $T_{min}$ | Mean temperature of the coldest month (°C) |
| $D_T$ | Range between $T_{max}$ and $T_{min}$ (°C) |
| $P$ | Mean total annual precipitation (mm) |
| $P_{max}$ | Mean total precipitation of the wettest month (mm) |
| $P_{min}$ | Mean total precipitation of the driest month (mm) |
| $P_{tmax}$ | Mean total precipitation of the warmest month (mm) |
| $MI$ | Moisture index: the ratio of P to annual potential evapotranspiration |

Whereas paleobiologists look to the ancient past for insight into the future, many field biologists interested in global warming look to the present to examine how biota are regulated by and respond to natural climate variability of a magnitude similar to that expected from global warming. Two approaches are used in this type of research. First, scientists can conduct “space-for-time” analyses along elevational or latitudinal gradients. This approach suggests that the effects of climate change over time on particular biota may be represented by current differences between the biota of interest and the same type of biota found at warmer, lower elevations or latitudes. Second, researchers who conduct multiyear studies at particular sites can monitor the response of biota to the natural interannual variability of climate. In particular, biotic responses to climate in more “normal” years can be compared to biotic responses to very warm years, droughts, early snowmelt, and other climatic events that fit predicted changes due to global warming. In some cases, researchers have access to records of climate and biota from several decades ago and can compare them to current records for the same sites.

This type of research has the advantage of actually studying current biota in the field in relation to climate, but it also has several disadvantages. For example, from one year to the next and from one place to another, sites vary not only in their climate but also in many other factors (e.g., land use history, species composition, topography), making it difficult to establish whether particular climate factors and/or other nonclimatic factors underlie observed patterns. Even if sites appear to differ primarily in climate, they may differ by predicted amounts of temperature but not by predicted changes in precipitation and soil moisture. Additionally, biota have had longer time periods to adjust and adapt to current climate variation at particular sites than they will have to adjust to climate change from global warming. Finally, this approach is unable to explore the effects of increased atmospheric CO$_2$ with the exception of some research on natural CO$_2$ gradients near hot springs.

### 4. Manipulations

Manipulations are one of scientists' most potent research tools. By conducting controlled manipulations of various climate, atmosphere, and other resource factors expected to change as a result of global warming, climate change researchers can work toward understanding the role of single or multiple factors and their interactions in changing ecosystem structure and function. This type of research is used to predict both how specific anthropogenic climate change scenarios might impact biota and how resulting ecosystem changes may pro-
duce feedbacks to the climate system. In climate change ecology, manipulative research falls into two types of approaches: microcosm experiments and field experiments. Microcosms, which generally take the form of laboratory growth chambers of various sizes, can be used to carefully manipulate particular global warming factors (e.g., temperature, moisture, light, nutrients, atmospheric composition) and to monitor the response of soils, single or multiple organisms, assembled simple ecosystems, or intact ecosystem cores taken from the field. Field experiments also manipulate global warming factors in order to look at interactions between climate change and biota, but do so in intact natural ecosystems (Fig. 5).

The strengths and weaknesses of these two approaches are interrelated. Although it is relatively easy to manipulate, control, and replicate microcosms, field experiments may be confounded by ecosystem variability and complexity. In field experiments, typically only a very few experimental variables can be manipulated, controls can be difficult to establish, and adequate replication is often expensive and time-consuming. However, field experiments have the advantage of being conducted in a natural setting at broader scales that may be more useful for drawing conclusions about complex, "real-world" ecosystem dynamics, compared to highly simplified and small-scale microcosm experiments. In both types of experiments, the relatively abrupt, short-term manipulation of climate may not be a good analog of anthropogenic climate change, which is occurring more gradually over decades and centuries. In addition, changes to disturbances such as fires and hurricanes may prove to be more important in determining the abundance and distribution of biota in many ecosystems than the usual experimental focus on "average" changes in variables such as temperature, moisture, and CO₂.

5. Integrated Research

Given the limitations of each type of research, the most productive strategies for exploring interactions between ecosystems and anthropogenic climate change integrate multiple research approaches. For example, responses of biota to natural climate variation can be compared to responses of the same biota to manipulated climate change to see how responses differ or stay the same over multiple spatial and temporal scales. Results from field experiments and gradient studies often suggest mechanisms that can be more thoroughly tested in microcosm experiments. Gradient, field experiment, and paleobiological data sets can be used to parameterize, calibrate, and validate models of biotic response. In general, the thoughtful integration of approaches can build on the strengths and avoid some of the limitations of each type of research, thus helping scientists to develop more rigorous hypotheses about global warming impacts and ecosystem feedbacks.

C. Impacts of Climate Change on Biota

1. Types of Responses of Organisms, Populations, and Species
   a. Adjustment
   The first level, short-term response of any organism to changes in their environment is adjustment, also referred to as acclimatization. All organisms have some

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FIGURE 5 Profile of a heated plot used in a long-term ecosystem warming experiment to investigate the interactions between climate warming and the ecology and biogeochemistry of a subalpine meadow ecosystem at the Rocky Mountain Biological Laboratory in Gothic, Colorado, U.S.A. The heaters increase downward infrared radiation flux (+ 22 W m⁻²) to a degree comparable to that expected under a 2 X CO₂ scenario. Layout of the plots is shown below; even-numbered plots have heaters and odd-numbered plots are control plots that lack heaters. (Adapted with permission from J. Harte and R. Shaw, Shifting dominance within a montane vegetation community: Results of a climate-warming experiment. Science 267, 876. Copyright © 1995 by AAAS.)
degree of physiological, life-history, or behavioral plasticity that enables them to live in a variable environment. The degree of plasticity with regard to climatic and atmospheric conditions varies widely among different kinds of organisms. Therefore, some types of organisms will be able to adjust to relatively large changes in climate, whereas others will be unable to adjust to even apparently minor increases in temperature or slight variations in precipitation.

An example of climatic adjustment in animals involves thermoregulation in vertebrates. Endotherms such as mammals have built-in physiological mechanisms to cope with body temperature changes. Ectotherms such as reptiles have behavioral traits that help regulate body temperature. Because of traits such as these, initial increases in environmental temperature should be well within the tolerances of many vertebrates. In plants, the concurrent increase of atmospheric CO₂ with surface temperature may augment the ability of some individuals, populations, and species to adjust to and flourish under anthropogenic climate change.

Increases in CO₂, especially for plants with the common C₃ photosynthesis pathway (e.g., most trees and shrubs), can result, at least initially, in the CO₂ fertilization effect mentioned before. Enhanced CO₂ concentrations can increase the ability of these types of plants to tolerate water stress, higher temperatures, and lower light. Other kinds of plants, particularly those with the C₄ photosynthesis pathway (e.g., many low-latitude and low-elevation grasses), have physiological mechanisms that enable them to withstand warm temperatures and low availability of water. Such mechanisms provide a means of adjustment to drought stress that may be associated with increased temperatures and evaporation.

While most biota will have at least some capacity to withstand, and in some cases benefit from, initial changes in climate, the rapid rate and large magnitude of climate change are likely to quickly surpass their capacity to adjust to new climate conditions within their pre-warming habitats. Biota that cannot continue to adjust will have to respond through evolution, migration, or extinction.

b. Evolution

Theoretically, populations and species could develop new adaptive traits as a result of evolution in response to anthropogenic climate change, thus enhancing the long-term survival of current taxa under new climate conditions. However, scientists generally agree that evolutionary responses to climate change are unlikely for most taxa since climate is changing rapidly compared to usual rates of evolutionary change. This view is supported by fossil data that reveal the morphological stasis of many taxa during previous periods of rapid climate change.

In the face of strong selectional pressure there is evidence that some species, especially those with fast generation times, can evolve very rapidly. For example, grass populations grown on soils polluted by heavy metals have shown signs of significant, genetic-based, heavy-metal tolerance within one or two decades. Some insects can evolve increased resistance to pesticides over the course of a few years. These types of responses depend on the presence of appropriate genetic variability in populations and species relative to a strong selective factor. As a result of global warming, populations and species will be exposed to novel environments resulting from climate change and associated shifts in ecosystem structure and function. Since many populations and species have climate-related genetic variability (e.g., differences in high temperature tolerance, drought tolerance), rapid adaptation is possible.

Will anthropogenic climate change actually result in directed selectional pressures that are strong enough to drive microevolutionary responses? For at least the next several hundred years, climate and species distributions are likely to be in fairly constant flux, which will tend to disrupt any potentially adaptive trends. Also, rapid evolutionary responses to anthropogenic climate change are unlikely in populations and species that have relatively long generation times, such as trees and many vertebrates. An added constraint on potential microevolutionary responses to global warming is the ongoing reduction in population size and thus genetic diversity of many species as a result of habitat destruction and other stresses. For most biota, other types of responses are far more likely to occur than evolution.

c. Migration

As current habitat becomes inhospitable owing to direct and indirect effects of climate change, biota will tend to track shifting climate and suitable habitat through dispersal and migration. Consequently, as a result of global warming, organisms are predicted to move generally poleward in latitude and upward in elevation. A rule of thumb is that a 3°C change in temperature is approximately equivalent to a move of 250 km of latitude or 500 m of elevation. However, migration will be restricted or made impossible to the extent that there are inherent (e.g., low mobility, slow reproductive rates) or external barriers (e.g., mountain ranges, large lakes) to movement (see Boxes 2 and 3).
Biota Most at Risk from Climate Change

Given our knowledge of climate change and biology, the kinds of biota most likely to be at risk from global warming over the next several decades and centuries can be characterized:

1. **Those at higher latitudes**: Scientists know with a high degree of certainty that temperature increases due to global warming will be greatest in polar regions. Therefore, higher-latitude temperate and Arctic/Antarctic ecosystems such as boreal forest, tundra, and peat bogs will experience both rapid and severe temperature increases, resulting in profound biotic change and disruption.

2. **Those on mountain-tops**: Temperature increases will also be greater at higher elevations. Montane biota will tend to move up in elevation as cooler, higher elevations warm. Biota already limited to mountaintops will be at serious risk of local extinction due to alteration of summit climate, the lack of potentially suitable habitat to migrate to, and the encroachment of lower-elevation species.

3. **Those in low-lying coastal areas and on islands**: Even small increases in sea level (i.e., several centimeters) can result in altered coastal marine dynamics and flooding of low-lying areas. Rising sea levels will destroy or cause severe damage to ecosystems at the terrestrial/marine interface, such as salt marshes, estuaries, mangroves, and sand dunes, and are likely to disrupt coastal marine food webs.

4. **Those sensitive to extreme disturbance events**: Even though disturbances such as fires and hurricanes are a natural part of ecosystem dynamics, any increases in frequency and intensity of such disturbances due to global warming are likely to disrupt biota. For example, ecosystems such as tropical montane forests may have less time to recover between hurricanes, limiting the development of slow-growing, late-successional species.

5. **Those with migration problems**: Because a major potential response of biota to climate change is to migrate to new areas, biota that lack the ability to readily disperse or move will be at a serious disadvantage. These include:

   a) plants whose seed or clone dispersal rates and animals whose movement rates lag behind rates of climate change;
   b) slow-growing populations and species that will not have time to adjust to new conditions;
   c) biota that cannot or are slow to cross geographic barriers, for example, fish in isolated lakes, low-elevation plants bounded to the north by mountain ranges, and tropical forest birds and insects that do not cross unforest ed areas;
   d) organisms that depend on other biota for habitat or food, but that have very different degrees of mobility;
   e) species such as monarch butterflies and migratory shorebirds that have multiple habitat requirements; and
   f) relic biota that have been left in small, unusual habitats by chance and have no nearby potential habitat.

6. **Those that are rare**: Populations and species with few numbers, low genetic variability, or limited or unusual ranges will be vulnerable to climate fluctuations and will be at increased risk of extinction. Also, unusual, unique ecosystems may break apart as populations and species respond in largely individualistic ways to climate change.

7. **Those dependent on particular hydrological regimes**: Though it is often uncertain at local and regional scales how and to what degree precipitation and moisture availability will change from global warming, it is quite certain that change will occur. Such changes could be critical in ecosystems such as tropical forests where the availability of food resources for animals is dependent on the timing of rainfall. In montane areas, many organisms will be very sensitive to changes to the snowpack and snowmelt.

8. **Those close to critical physiological thresholds**: Many organisms are adapted to living within a narrow range of limits of temperature, moisture, nutrients, light, and atmospheric composition. Others have wider tolerances but are already operating close to a threshold, beyond which their ability to live, grow, and reproduce is severely limited. Climate change may force the environment past such limits for some organisms, resulting in severe im-
pacts, especially if dispersal or growth is slow. For example, slight increases (1–2°C) in surface water temperature can induce bleaching and mortality of coral reefs, which have very slow rates of growth and provide habitat for many marine species.

9. Those that have highly specialized relationships with other organisms: Some species depend entirely on just one or a very few other species for nourishment or reproduction. If species respond very differently to changes in climate than do the species they depend on, and they cannot substitute other organisms to fulfill those roles, they will go extinct.

10. Those negatively affected by other anthropogenic stresses: Humans engage in many activities that result in deleterious impacts such as acid deposition, pollution, ozone depletion, and alien species introduction. When organisms are weakened by one of these stresses, they tend to become even more vulnerable to other stresses such as global warming. For example, insect pests can damage vegetation more when pollutants reduce plants' resistance to herbivory and warmer temperatures encourage pest population growth. If those insect pests happen to be alien, they may cause even more damage owing to lack of local predators and because local plants may lack resistance to alien pests. Also, changes in land use such as deforestation can reduce and isolate populations as well as create barriers to migration through habitat fragmentation and destruction.

Fossil records show that for many types of organisms, warming during the last deglaciation induced significant changes in latitude and elevation of species' ranges (Fig. 6). Those distributional changes sometimes occurred at very rapid rates. For example, peak migration rates for some tree species in North America during the last deglaciation reached 100–500 m per year, probably as a result of haphazard, long-distance transport of seeds by animals, storms, or water (Clark et al., 1998). However, even these very fast historic migration rates only translate into 10–50 km per century, whereas anthropogenic climate change will likely require latitudinal shifts of at least 200–300 km over the next century. In some cases, changes in potential range bound-

### Box 3

**Biota That May Benefit from Climate Change**

Because of the slow rate of most evolutionary responses, including speciation, there are few ways that global warming could augment global biodiversity over the next several hundred years. However, climate change will benefit some biota through increases in abundance and range expansions, often at the expense of more at-risk biota. Types of biota likely to benefit from climate change include:

1. Those that migrate easily: Biota that are highly mobile and have rapid dispersal rates, such as some kinds of winged insects, will be equipped to track changing climate.

2. Those that are opportunistic: Opportunistic organisms that can colonize disturbed areas will be at an advantage because they will be able to migrate through marginal habitat and establish in climatically disrupted ecosystems. For example, global warming is expected to promote the spread of already weedy introduced plant species, and may facilitate the escape of more garden cultivars into natural ecosystems.

3. Those that are ecological generalists: Organisms that flourish in a wide variety of environments and have either wide tolerances for variable resource availability and climate or many possible prey items will fare better than highly specialized organisms.

4. Those that have high variability and rapid reproduction: Populations and species with lots of phenotypic or genetic variation and rapid reproductive rates have the best chances of adjusting and adapting to rapidly changing climate.

5. Those favored by new optima: Although climate and atmospheric conditions will shift away from optima for many organisms, more optimal conditions will be created for other organisms. For example, temperature increases are expected to increase parasite and insect development time, allowing parasites to spread with migrating insect hosts and promoting pest infection and parasite infection of new hosts. These types of responses may lead to range expansions of agricultural pests and disease transmissions, as well as more frequent outbreaks (Dobson and Carper, in Peters and Lovejoy, 1992).
FIGURE 6 Maps of observed (upper row) and simulated (lower row) percentages for spruce tree pollen in eastern North America over the last 18,000 years. The simulated spruce pollen maps are based on the modern response of spruce pollen percentages to July temperature, January temperature, and precipitation as applied to simulated historical climates. Dark shading indicates the highest abundance of spruce. (Reprinted with permission from T. Webb, Ill. Past changes in vegetation and climate: Lessons for the future, in Peters and Lovejoy, 1992. As adapted with permission from COHMAP Members. (1988). Climatic changes of the last 18,000 years: Observations and model simulations. Science 241, 1043. Copyright © 1988 by AAAS.)

The rapid pace of anthropogenic climate change will easily outstrip the capacity of some organisms to move or disperse to suitable new habitat. In addition, human destruction of habitat will create insurmountable barriers to migration for biota that have difficulty crossing large areas of urban development or agricultural use. In the short run, any migration that does occur may tend to increase local levels of biodiversity in some ecosystems as new species move in before old species completely migrate or die out. This lag effect will tend to disappear with time.

d. Extinction

Biota that are unable to adjust, evolve, or migrate are unlikely to survive long in their pre-warming habitats. As a result of climate change, organisms may be exposed to increasing physiological stress, be abandoned by their mutualists and prey, be outcompeted by more flexible neighbors or incoming species, and be attacked by new predators and pests. Although microevolutionary responses are possible for some populations, rapid genetic adaptation is likely to occur in very few. Many species will be faced with migration problems. Even in species that successfully migrate, some populations are likely to go extinct, particularly at southern and lower edges of species' ranges, reducing genetic variability. Extinctions attributable primarily to global warming will be few over the next several decades, but will undoubtedly increase dramatically as time passes, climate change intensifies, and biotic response options narrow.

2. Impacts on Biotic Assemblages

A key insight from the fossil record is that species tend to respond to climate change individualistically rather than as a group. Thus, while the general trend is for species to move poleward and to higher elevations as climate warms, particular species can vary quite dramatically in how fast and how much their ranges contract, expand, or move, what directions they move in, and at what rate they move around or over barriers such as mountain ranges. Consequently, past communities repeatedly disassociated and re-sorted into novel combinations. In some cases, although the same species still exist, there are no modern examples of historic species associations. For example, for several thousand years at the end of the last glacial period, spruce trees grew in open parklands in association with sedges. Today spruce is found in a completely different ecosystem type, the closed-canopy
boreal forest, in association with birch, alder, and fir (Webb, in Peters and Lovejoy, 1992). Anthropogenic climate change is likely to result in the reconstitution of communities and ecosystems in unexpected ways.

Biota tend to move individualistically in response to long-term climate change because tolerances to climatic and atmospheric conditions are often specific to the organism, population, or species. Individualistic responses can lead to apparently counterintuitive shifts in range, especially if temperature is not the primary determinant of distribution. For example, the distribution of the gopher tortoise during the most recent deglaciation shifted south, rather than north. One hypothesis for this pattern is that seasonal climate extremes increased with warming, and that these extremes were more important for determining tortoise distribution than warming (Graham, in Peters and Lovejoy, 1992).

In addition to climate and atmosphere, other abiotic factors (e.g., soil type, topography, disturbance regime, site history) and biotic interactions (e.g., mutualism, competition, predation, pollination) can play significant roles in determining the abundance and distribution of biota in both the short and long term. The interplay of all of these factors over time can result in complex and often unpredictable changes in the distribution, abundance, and diversity of biota.

Global warming will also precipitate many asynchronies that reduce the ability of biota to respond effectively to climate change. "Asynchrony" refers to a mismatch in timing or rate of change. One type of asynchrony already discussed is the mismatch between very rapid rates of anthropogenic climate change and slower rates of dispersal and migration for many species. Another type of asynchrony due to global warming is the potential mismatch between required resources and the availability of resources. Organisms are embedded within a network of relationships with other organisms, which they may depend on for sustenance and reproduction. However, different types of organisms may be affected very differently by climate change, which can disrupt biotic relationships that are important for community and ecosystem dynamics. For example, many species of flowering plants depend on specific animal pollinators such as butterflies, hummingbirds, and bees for successful reproduction, and the pollinators depend on those plants for food. In a hypothetical example, if the timing of flowering in a plant is primarily determined by early season temperature, while the emergence and activity of its pollinator is primarily determined by the amount of daylight, the shifting of temperature but not light levels due to global warming could lead to the pollinators being active after the plants flower. This type of

![FIGURE 7 Current geographical range (horizontal lines) and potentially suitable range under doubled CO₂ (vertical lines) for beech trees in North America. Cross-hatched lines indicate areas of overlap between current and potential future ranges. (A) Output for a milder climate change scenario and (B) output for a more severe climate change scenario. (Adapted with permission from M. B. Davis and C. Zabiniski, 1992, Changes in geographical range resulting from greenhouse warming: Effects on biodiversity in forests, in Peters and Lovejoy, 1992. Copyright © 1992 by Yale University Press.]

asynchrony can reduce the reproduction and abundance of the plants, and reduce the availability of food for the pollinators. If the species involved are highly specialized on each other, they are likely to go extinct.

**D. Evidence for Current Global Warming Impacts on Biota**

During the 1990s, researchers started reporting the first evidence that global warming during the twentieth century has begun to influence populations, species, and ecosystems (see Box 4 for a bibliography of the sources cited in this section). Some evidence comes from coastal marine systems. Roemmich and McGowan (1995) reported that since 1951, zooplankton biomass in coastal southern California waters had decreased by 80% over four decades, at the same time that surface water layers warmed more than 1.5°C in some areas. They suggested that the surface warming resulted in changes to stratification and the thermocline that led to a reduction in upwelling of nutrients and thus primary production by phytoplankton, the ultimate food source of zooplankton. Barry and colleagues (1995) compared changes in abundances of 45 invertebrate species in a central California intertidal community from the 1930s to the 1990s. During that period of time, annual mean shoreline temperature at the study area increased by 0.75°C, and average summer temperature increased by 2.2°C. Eight of nine species with a southern geographic range showed significant increases in abundance, whereas five of eight species with a northern distribution showed significant decreases. Species with wide distributions showed no strong patterns of change.

At high elevations and latitudes, terrestrial vegetation appears to be responding to the warmer climate. Grabherr and colleagues (1994) compared 40- to 90-year-old records of plant distribution on high-altitude mountaintops (~2900 to 3500 m) in the Alps to 1992 data, given a 0.7°C increase in mean annual temperature during that time period. They found upward migration rates by nine “typical” species of <1 to 4 m per decade. In addition, species richness increased over time, with the increase most pronounced at lower-altitude summits. Myneni and colleagues (1997) presented evidence from satellite data from 1981 to 1991 that suggests that the photosynthetic activity of terrestrial vegetation in northern high latitudes increased by 7–14% over that time period. This increase may indicate an intensification of plant growth associated with a 12-day increase in the growing season.

Insect species are also displaying sensitivity to recent climate change. Parmesan (1996) examined historical records and recorded the current status of 151 populations of Edith’s checkerspot butterfly throughout its entire range. She found that net extinctions of populations were significantly greater at southern latitudes and lower altitudes, resulting in an observed northward and upward shift in the species’ range during the last several decades. In a later study that examined range shifts in 33 nonmigratory European butterfly species during the last century, Parmesan and colleagues (1999) reported that 63% of the species displayed northward range shifts of 35 to 240 km, while only 3% shifted south.

Vertebrates also appear to be sensitive to recent climate change. Current evidence suggests that birds are both breeding earlier and shifting their ranges northward in response to warming. Brown and colleagues (1999) found that from 1971 to 1998, the average timing of first clutch in the Mexican jay in Arizona occurred 10 days earlier. This change was associated with significant increases in monthly minimum temperatures. Crick and Sparks (1999) studied 20 United Kingdom...
bird species over 25 years and found long-term trends toward earlier egg laying in most species. A data set of 36 bird species over 57 years suggests that 86% of the species display significant relationships between timing of egg laying and temperature or rainfall. Furthermore, Thomas and Lennon (1999) examined the breeding distributions of British birds over a recent 20-year period and found that the northern margins of the species’ ranges moved north by an average of 19 km.

In general, the observations of all of these studies are consistent with predictions of impacts of climate change on biota, and demonstrate how just a small amount of climate change over brief time periods can lead to significant ecological changes.

VI. CONCLUSIONS

The enhanced greenhouse effect, in conjunction with other anthropogenic stresses, is likely to precipitate unprecedented changes to Earth’s climate and ecosystems. Though the details of how climate change will affect biodiversity are often hard to predict, there is little doubt that biological impacts will be pervasive and often dramatic. Studying the effects of climate change on biota can help in the formulation of strategies for conserving biodiversity and ecosystem structure and function in the face of potentially massive change and loss. Such knowledge is also crucial for refining predictions of the future rate and magnitude of global warming, since biological responses are likely to produce significant feedbacks that can augment or dampen climate change at local, regional, and global scales. Understanding and addressing the interactions between climate change and biodiversity represents one of the greatest challenges that scientists and policymakers will face in the twenty-first century.

See Also the Following Articles

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Bibliography


