Greenhouse Effect

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Introduction

Earth’s climate, from daily average 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 follows one of three pathways: absorption by the atmosphere (25%), reflection back into space (30%), or absorption by the earth’s surface (45%). The light absorbed by earth’s surface and by the atmosphere is converted from shortwave visible light to energy in the form of longwave infrared radiation (i.e., heat). Several gases in the atmosphere, referred to as “greenhouse gases,” absorb some of the heat and re-radiate it back toward the surface, increasing surface temperature. Without this naturally occurring greenhouse effect, Earth’s average surface temperature would be approximately −18 °C, about 33 °C colder than it is today.

It should be noted that while the atmospheric greenhouse and actual physical greenhouses both trap heat, they do so via different mechanisms. A physical greenhouse traps air inside the building so that its heat cannot escape by convection; the atmospheric greenhouse absorbs the heat in gas molecules and re-radiates it back toward the earth’s surface.

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 halocarbons, 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 1; Figure 1), 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 re-radiate more heat, resulting in rising surface temperature and other climatic changes.

Increases in CO2 account for about half of the current direct positive radiative forcing due to anthropogenic emissions (Figure 2). The atmospheric CO2 concentration has increased by 35% since preindustrial times, as a result of emissions from fossil fuel combustion, land conversion, and cement production, and is continuing to increase by 0.5% per year (Figure 2). If future emissions of CO2 were maintained at 2005 levels, CO2’s atmospheric concentration would be roughly double the preindustrial level by the end of twenty-first century. Concentrations of other greenhouse gases, particularly methane and nitrous oxide, also continue to slowly rise. Greenhouse gases tend to remain in the atmosphere for

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 carbon dioxide (CO2) concentration in the atmosphere versus its preindustrial (1750) level.
Earth energy balance Difference (if any) between incoming solar energy and outgoing terrestrial radiation for Earth as a whole.
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 re-radiate infrared radiation.
Litter Dead organic matter, such as leaves and branches, that is deposited as the top soil layer.
Radiative forcing Measure used to express and compare the potential of climate system changes (vs. preindustrial) to perturb the Earth’s 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.
Sink A physical reservoir of a compound that can take up additional quantities of this compound from the air and thus reduce its atmospheric concentration; for example, trees are a sink for CO2.
In addition to greenhouse gases, fine particles suspended in the air called aerosols can also affect the climate. Aerosols can be produced by natural sources such as dust and sea spray, and can also be produced by human activities such as incomplete combustion of fossil fuels and biomass. Aerosols can alter the climate by changing atmospheric albedo. These fine particles can both reflect and absorb solar radiation and alter cloud properties to produce a net cooling effect. The overall effect is usually one of cooling, although atmospheric soot over snow or ice can warm regionally. The current estimate of the combined effect of aerosols is $\sim 1.2 \text{ W m}^{-2}$ compared to $3 \text{ W m}^{-2}$ due to greenhouse gases (Figure 1). Aerosols are very short-lived in the atmosphere (days to weeks) and respond rapidly to changes in emissions.

**Climatic Consequences: Global Warming**

**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 CO$_2$ concentrations (Figure 3). The historical swings between Ice Ages and warm periods are triggered by periodic, predictable changes in the tilt of Earth’s axis, the direction of its axis relative to the sun, and the shape of its orbit. The initial trigger created by these changes produces biological feedbacks that will be discussed in the Section, Feedbacks. These feedbacks change the amount of CO$_2$ in the atmosphere, and the resulting greenhouse effect amplifies the initial warming or cooling.
Radiative forcing of climate between 1750 and 2005

Radiative forcing terms

<table>
<thead>
<tr>
<th>Category</th>
<th>Description</th>
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<tr>
<td>Long-lived greenhouse gases</td>
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<td>Ozone</td>
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<td>Stratospheric water vapour</td>
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<td>Cloud albedo effect</td>
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<td>Natural processes</td>
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<td>Solar irradiance</td>
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<td>Total net human activities</td>
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Figure 2 Estimates of the globally and annually averaged radiative forcing due to anthropogenic changes in concentrations of greenhouse gases and aerosols and natural changes in solar output from preindustrial times to 2005. The length of the rectangular bars indicates a midrange estimate of forcing, and the error bars show an estimate of the uncertainty range. The level of scientific understanding is rated by the IPCC as "high" for the long-lived greenhouse gases, "med" for ozone, "med–low" for surface albedo and aerosol direct effect, and "low" for stratospheric water vapor, aerosol cloud albedo effect, linear contrails, and solar irradiance. Reprinted from FAQ 2.1, Figure 2 in Forster PM, Ramaswamy V, Artaxo P, et al. (2007) Changes in atmospheric constituents and in radiative forcing. In: Solomon S, Qin D, et al. (eds.) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press. Caption information from Figure 2.20 in the same report.

Figure 3 Variation during the last 450,000 years of atmospheric CO₂ and CH₄ concentrations and atmospheric temperature, as derived from the Vostok, Antarctica ice core. Note that the temperature change is that of an average over the higher latitudes of the southern hemisphere (roughly 45 to 90°S) and that polar regions experience larger temperature swings than the earth overall. Reprinted with permission from Figure 2.31 of Wallace JB and Hobbs PV (2006) Atmospheric Science: An Introductory Survey. Amsterdam, The Netherlands: Academic Press.
Recent Climate Change

Observational data provides clear evidence of human-induced global warming. Global average surface temperature trends reveal a 0.7 °C temperature increase during the past hundred years, with the 10 hottest years on record between 1880 and 2010 occurring between 1998 and 2010.

How do the recent temperature increases compare to natural climate variability? The key drivers of natural climate variability are orbital patterns, solar cycles, and volcanic eruptions. The first two are predictable and are included in climate model projections. Volcanic eruptions are included in retrospective models. Figure 4 illustrates the amount of temperature change attributable to natural variation (in blue) relative to the total change observed (black line) and the total change predicted (in pink). This diagram illustrates that most of the change experienced during the past century is attributable to human activity and also shows that models can do a good job of replicating past climate system behavior. This ability of models to faithfully reproduce the past provides evidence that they have some predictive power for the future.

Future Climate Change

What will the future bring? Future climate will depend in part on societal decisions about future emissions and in part on emissions that we have already generated. The climate system includes two important time lags. First, long-lived emissions like CO₂ stay in the atmosphere for decades or centuries after the initial release. Second, Earth’s heat builds up gradually over many years, creating a slow rise in Earth’s temperature. These two factors explain why the emissions produced today commit the planet to a warming trajectory that extends decades into the future.

General circulation models (GCMs) integrate the physics of radiative forcing, ocean dynamics, and other complex Earth–atmosphere processes in order to simulate and predict the climate trends. Figure 5 illustrates the global average temperature trajectory for the period 1900–2100 under several different scenarios for anthropogenic emissions. The orange line illustrates the slight temperature increase that would result if atmospheric concentrations were held constant (i.e., emissions were dramatically reduced to a replacement-rate level). The other lines illustrate scenarios with higher levels of emissions. Note that the graph shows only the global average, but temperature change is greater at the poles.

As of 2010, society is on a path that is in line with the upper emissions scenarios. Temperatures are projected to rise by approximately 1.5 °C versus preindustrial by 2030 and by 2 °C versus preindustrial by 2050. The threshold for “dangerous anthropogenic interference” (DAI) is considered to be 2 °C. This threshold has international political significance: the Kyoto Protocol (1997), the Copenhagen Accord (2009), and the Cancun Agreements (2010) are agreements by national governments to take the necessary steps to avoid crossing the threshold of DAI.

The impacts of climate change include effects on agricultural productivity, availability of freshwater, spread of disease, extreme weather events, alteration of ecosystems, and loss of biodiversity (see Climate Change and Biodiversity). Climate models 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, with greater warming at the poles than at the equator. Winter temperatures are expected to increase more than summer temperatures, and night-time 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, patterns of precipitation and soil moisture will change. Warming is predicted to increase evaporation and global mean precipitation, and may increase cloud cover. Geographic distribution of precipitation is expected to shift in patterns that are not yet predictable. High and middle latitudes and elevations will experience more winter precipitation falling as rain, earlier...
snowmelt, and reductions of summer soil moisture in non-coastal areas. Third, the frequency and intensity of extreme weather and disturbance events (e.g., drought, deluge, summer heat waves, hurricanes, and fires) are expected to increase. Fourth, average sea level is expected to rise 0.2–2.0 m during this century from a combination of thermal expansion, glacier melt, and ice sheet melt.

Some of these trends have already been observed. For example, more warming has occurred near the poles (2°C versus the global average), hot days and heat waves have become more frequent, cold days have become less frequent, droughts have increased in length and intensity, snowpack is decreasing and snowmelt is occurring earlier at high latitudes and elevations, glaciers are retreating, and sea levels are rising (sea level rose 17 cm during the twentieth century, mostly attributable to anthropogenic climate change).

While some climate changes follow a smooth, predictable trajectory (e.g., global average temperature), other changes are more abrupt. Tipping points occur when a major shift in a tipping element results from a small incremental change in the climate. Examples of potential tipping elements include loss of Arctic summer (September) sea ice, a shift in the monsoons (India, Sahara/Sahel, West Africa) or El Nino patterns, a shift in the Atlantic Ocean circulation, loss of the Greenland or West Antarctic ice sheets, or loss of the Amazon rainforest (due to precipitation shifts). Any one of these changes would have large-scale effects on the rest of the climate system via feedback loops (discussed below) and on biodiversity. While scientists have some broad estimates of the temperatures at which these tipping points could occur, the exact tipping points and associated time lags are highly uncertain.

**Feedbacks**

Climate change can trigger a variety of responses to biotic and abiotic processes, which results in changes in the flow of energy and greenhouse gases between the surface and the atmosphere. As a result of these responses, climate change resulting directly from anthropogenic emissions of greenhouse gases triggers further climate change. These feedbacks are reviewed below.

**Geophysical Feedbacks**

General circulation models include not only mechanisms underlying direct greenhouse gas and aerosol radiative forcing, but also mechanisms underlying the three large geophysical 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 water vapor acts as a greenhouse gas to 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 absorbs more sunlight, which augments warming.

Cloud formation adds much of the uncertainty to GCM estimates. If clouds form over highly reflective surfaces (e.g., ice and snow), they reduce the planet’s albedo. If they form over low-reflective surfaces (e.g., oceans and forests), they increase the planet’s albedo. In addition to uncertainty over where clouds will form, their longevity (before raining out),
height, and shape are also highly uncertain. In short, it is unclear whether there will be more clouds and if so, whether they will have characteristics that create warming or cooling. Currently, model estimates of the cloud feedback effect range from a slight negative feedback to a large positive feedback.

**Biogeochemical Feedbacks**

Biogeochemical feedbacks are those in which the ecosystem responses to climate changes influence the atmospheric concentrations of greenhouse gases and aerosols or the planet’s albedo, which in turn influence the climate. Examples of these feedbacks include: higher rates of decay of organic matter at higher temperatures (increases CO₂), release of methane from melting permafrost (increases CH₄), northward shift of shrubs and boreal forest due to amenable growing conditions (reduces albedo), and increased dust storms due to droughts (increase dust aerosols). Over the past few years, GCMs have been expanded to incorporate many biogeochemical feedback effects and their overall effect is to increase the rate of warming (a positive feedback effect). Many biogeochemical feedbacks due to climate change also interact with other anthropogenic stresses, such as deforestation and pollution, to further influence climate change effects at local, regional, and global scales.

**Marine Feedbacks**

Climate change is likely to drive many complex marine-based feedback processes, of which only a few are mentioned here. With regard to geochemistry, warm water holds less dissolved CO₂ than cooler water; thus the warming of ocean surface waters expected under climate change will result in a positive feedback since a warmer ocean will release CO₂ to the atmosphere. Because oceans hold approximately 50 times as much carbon in the form of dissolved CO₂ and bicarbonate (HCO₃⁻) as there is CO₂ in the atmosphere, this effect could add 1° or 2°C to the predicted equilibrium warming. 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 called phytoplankton, which form the base of the oceanic food web. Through the process of photosynthesis, CO₂ is fixed by the phytoplankton and thus transferred from the atmosphere to ocean surface waters. Some of this 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 CO₂ in the atmosphere that is currently about 40% lower than it would be in the absence of marine organisms.

**Terrestrial Feedbacks**

Three to five 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 CO₂ 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 “CO₂ fertilization effect,” which refers to the stimulation of photosynthesis by increased levels of CO₂, which in turn can result in increased plant growth and greater storage of carbon in vegetation. This effect is limited to situations in which water and other nutrients are available in sufficient supply so that CO₂ is the limiting growth factor.

Climatic changes that will accompany higher concentrations of CO₂ make it even more complicated to predict the net effect of climate change on the storage of carbon in vegetation and soil versus the atmosphere. For example, under climate change, changes in water availability and temperature will reduce the CO₂ 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 CO₂ 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 climate change will result in reductions of terrestrial carbon storage, a positive feedback. Those same fires, however, will in many cases increase albedo (by reducing dark forest), a negative feedback. The net effect of fire can be a positive or negative feedback in different locations, and can change over time as the plant community composition changes postfire.

Another set of climate change 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 climate change will add dust to the atmosphere, like anthropogenic aerosols, that 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.

Climate Change and Biodiversity

Introduction

Currently, the largest reductions in biodiversity result from massive deforestation in the tropics, in conjunction with other sources of worldwide habitat destruction. Even as the razing of vast tracts of tropical forests is expected to lead 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. Climate change 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. If we assume conservatively that climate change 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 100,000 years, and a 4 °C increase would result in the warmest world in 40 million or more years. Second, climate change 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 climate change, but on generic ways in which biota will be affected by climate change 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.

How Scientists Study the Effects of Climate Change on Biota

Species Distribution 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, 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 species and bioclimatic variables that explicitly incorporate drought stress and seasonality (Table 2). These types of static models, referred to as “climate envelope models” can be used for single species or for life zones. They are constructed from comparisons of the current locations of species of vegetation or animals and climate and can then be used in conjunction with maps of simulated future climate to predict shifts in distribution of species due to climate change. The Holdridge life-zone classification has been used to predict the conversion of much of today’s boreal forest into temperate deciduous forest. While climate envelope models provide a way to look at the potential global-scale shifts in the distribution of plants or animals under climate change, they are limited in their applicability by a number of factors.

- Novel climates, consisting of combinations of, say, temperature and rainfall that are not found in today’s climate, may arise in the future.
- Nonclimatic factors, such as soil type, can limit the ability of vegetation to track shifting climate.
- Species interactions, such as those between plants and pollinators, are often critical to the ability of species to survive; if a plant but not its pollinators can disperse to a new geographic location with suitable climate, it will not be able to establish there.
- Climate envelopes are often constructed from locations of adult plants but the climate conditions may be limiting germination or seedling survival, not adult plants.
- Climate envelopes generally assume that all individuals in a species share the same preferences for climate, whereas populations within a species found across a range of climates may be adapted to local climate.

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Bioclimatic variables used by Box to predict distribution limits of plant types</th>
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<tr>
<td>T&lt;sub&gt;max&lt;/sub&gt;</td>
<td>Mean temperature of the warmest month (°C)</td>
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<td>T&lt;sub&gt;min&lt;/sub&gt;</td>
<td>Mean temperature of the coldest month (°C)</td>
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<td>D&lt;sub&gt;T&lt;/sub&gt;</td>
<td>Range between T&lt;sub&gt;max&lt;/sub&gt; and T&lt;sub&gt;min&lt;/sub&gt; (°C)</td>
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<td>P</td>
<td>Mean total annual precipitation (mm)</td>
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<td>P&lt;sub&gt;max&lt;/sub&gt;</td>
<td>Mean total precipitation of the wettest month (mm)</td>
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<td>P&lt;sub&gt;min&lt;/sub&gt;</td>
<td>Mean total precipitation of the driest month (mm)</td>
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<tr>
<td>P&lt;sub&gt;max&lt;/sub&gt;</td>
<td>Mean total precipitation of the warmest month (mm)</td>
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<tr>
<td>MI</td>
<td>Moisture index: the ratio of P to annual potential evapotranspiration</td>
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Species face many threats besides climate change, including habitat destruction, pollution such as acid rain, invasion of exotic species, and hunting or fishing pressure, and these threats can act synergistically with climate.

Simulation models, the other major modeling approach, incorporate and link multiple factors such as life-history traits, physiological constraints, biotic interactions, resource availability, and climate in order to predict dynamic changes in biota over the course of time. By using characteristics of individuals, populations, species, or functional types in conjunction with predicted changes in climate, modelers can simulate continuous vegetation responses to climate change at scales that vary from changes within a stand of plants to changes at landscape, regional, and global levels. Vegetation models can be used in turn to look at the changes in habitat and dynamics of other types of organisms. Simulation models not only attempt to predict patterns of change, but also provide means to explore how and why such change might occur. However, these analyses are often constrained by data requirements. Detailed and accurate information may not be available about the biota and environment of interest, and as simulations are scaled up to look at global impacts, specificity is lost. No matter how well models appear to fit observed dynamics, some factors not included in the model may be important for future dynamics, or the model may fit observed dynamics for the wrong reasons, rendering model predictions inaccurate.

Paleobiology
Paleobiologists combine historical climate and biological data to reconstruct past relationships between changes in climate and species distributions. Paleobiological data sources range from ice and soil cores to plant and animal fossils to tree rings and slow-growing corals. Such studies reveal the long-term and integrated direct and indirect effects of past climatic and atmospheric change on past biota and thus facilitate projections about how present-day biota might respond in the long term to anthropogenic climate change. Many crucial insights about previous and potential effects of climate change have emerged from this type of work (see Impacts of Climate Change on Biota). However, the generality of these types of studies is limited by the lack of good fossil records for many organisms and strict climatic parallels in the past to both the rate and magnitude of anthropogenic climate change, and by differences in the biology and geology of ancient times compared to the present. In addition, the interactions of climate change with other anthropogenic stresses such as pollution, development, agriculture, and deforestation are novel and not represented in the paleorecord.

Natural Climate Variability
Whereas paleobiologists look to the ancient past for insight into the future, many field biologists interested in climate change 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 climate change. 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 climate change. 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 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 different climate changes. Finally, this approach is unable to explore the effects of increased atmospheric CO₂, with the exception of some research on natural CO₂ gradients near hot springs.

Manipulations
Manipulations are one of scientists’ most potent research tools. By conducting controlled manipulation of various climate, atmospheric, and resource conditions expected to change as a result of 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 produce 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 climate change 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 factors in order to look at interactions between climate change and biota, but do so in intact ecosystems (Figure 6).

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 experiment, the relatively abrupt, short-term (months to decades) manipulation of climate may not be a good analog of anthropogenic climate change, which is occurring 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.

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...
Impacts of Climate Change on Biota

Types of Responses

Adjustment

The first level, short-term response of any organism to changes in its environment is adjustment, also referred to as acclimatization. All organisms have some 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 CO\(_2\) with surface temperature may augment the ability of some individuals, populations, and species to adjust to and flourish under anthropogenic climate change. Increases in CO\(_2\), especially for plants with the common C\(_3\) photosynthesis pathway (e.g., most trees and shrubs), can result, at least initially, in the CO\(_2\) fertilization effect mentioned above. Enhanced CO\(_2\) 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 C\(_4\) 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 prewarming habitats. Biota that cannot continue to adjust will have to respond through evolution, migration, or extinction.

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 climate change, 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 evolution 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, 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 climate change 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.

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 climate change, 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 barriers (e.g., low mobility, slow reproductive rates) or external barriers (e.g., mountain ranges, large lakes) to movement.

Fossil records show that for many types of organisms, warming during the last deglaciation induced significant changes in latitude and elevation of species’ ranges (Figure 7). 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. 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 boundaries resulting from climate change due to doubled CO\(_2\) may exceed 1000 km. For example, suitable habitat for beech trees, which currently grow over...
most of the eastern third of the US, could shift almost completely out of the country and into a much smaller area of the Northeastern US and Southeastern Canada as a result of a $2\times CO_2$ atmosphere (Figure 8). The rapid pace of anthropogenic climate change will easily outstrip the capacity of some organisms to move or disperse to a 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

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**Figure 7** 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 from Webb T III (1992) Past changes in vegetation and climate: Lessons for the future. In: Peters R and Lovejoy T (eds.) Consequences of Global Warming for Biological Diversity, pp. 59–75. New Haven, CT: Yale University Press, and adapted from Figure 5 in COHMAP Members (1988) Climatic changes of the last 18,000 years: Observations and model simulations. Science 241, 1043–1052.

**Figure 8** Current geographical range (horizontal lines) and potentially suitable range under doubled $CO_2$ (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 from Figure 5.6 in Davis MB and Zabinski C (1992) Changes in geographical range resulting from greenhouse warming: Effects on biodiversity in forests. In: Peters and Lovejoy, with permission from Yale University Press.
migrate or die out. This lag effect will tend to disappear with time.

**Extinction**

Biota that are unable to adjust, evolve, or migrate are unlikely to survive long in their prewarming habitats. As a result of climate change, organisms may be exposed to increasing physiological stress, abandoned by their mutualists and prey, outcompeted by more flexible neighbors or incoming species, and 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 climate change will be few over the next several decades, but will increase dramatically as time passes, climate change intensifies, and biotic response options narrow.

**Types of Biota Impacted**

**Organisms at Risk**

Given our knowledge of climate change and biology, the kinds of biota most likely to be at risk from climate change over the next several decades and centuries can be characterized. They include organisms that live in particular types of habitats such as at higher latitudes, on mountaintops, in low-lying coastal areas, or on islands. Scientists know with a high degree of certainty that temperature increases due to climate change 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. Temperature increases will also be greater at higher elevations. Montane biota will tend to move up to cooler elevations. 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. Additionally, even small increases in sea level (i.e., several centimeters) due to climate change 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.

Biota that lack the ability to readily disperse or move will be at a serious disadvantage. These include plants whose seed or clone dispersal rates and animals whose movement rates lag behind rates of climate change; slow-growing populations and species that will not have time to adjust to new conditions; 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 unforsted areas; organisms that depend on other biota for habitat or food, but that have very different degrees of mobility, species such as monarch butterflies and migratory shorebirds that have multiple habitat requirements; and relic biota that have been left in small, unusual habitats by chance and have no nearby habitat.

Organisms that are sensitive to extreme disturbance events, dependent on particular hydrological regimes, or that have certain kinds of physiological tolerances are also likely to be negatively impacted by climate change. 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 climate change 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. In terms of hydrological cycles, though it is often uncertain at local and regional scales how and to what degree precipitation and moisture availability will result from climate change, it is quite certain that changes 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 in the snowpack and snowmelt. Regarding physiological tolerances, some organisms are adapted to living within a narrow range of limits of temperature, moisture, nutrients, light, and atmospheric composition, while 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 physiological limits for some organisms, resulting in severe impacts, 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.

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. Taxa that have highly specialized relationships with organisms are also at risk. 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. Unusual or unique ecosystems may break apart as populations and species respond in largely individualistic ways to climate change and as feeding and other species interactions are disrupted.

Finally, climate change may negatively impact taxa that are already being challenged by other anthropogenic stresses. Humans engage in many activities that result in deleterious impacts such as habitat destruction, 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 climate change. 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.
**Organisms Likely to Benefit**

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 those that migrate easily, are opportunistic or generalists, or have high variability and rapid reproduction. Biota that are highly mobile and have rapid dispersal rates, such as some kinds of winged insects, will be equipped to track changing climate. 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, climate change is expected to promote the spread of already weedy introduced plant species, and may facilitate the escape of more garden cultivars into natural ecosystems. Generalist 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. Also, 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. Finally, some organisms will be favored by new optima that result from climate change. For example, temperature increases are expected to increase parasite and insect development time, allowing parasites to spread with migrating insect hosts and promoting pest infestation 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.

**Impacts on Communities**

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 for species is 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. 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.

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.

Climate change 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 climate change 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 climate change could lead to the pollinators being active after the plants flower. This type of 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. These types of disruptions to species interactions can potentially alter the structure, dynamics, and stability of entire food webs and other ecological networks such as pollination and seed dispersal networks.

**Evidence for Current Climate Change Impacts on Biota**

During the 1990s, researchers started reporting the first evidence that climate change during the twentieth century has begun to influence populations, species, and ecosystems (see Box 1 for a bibliography of the sources of information included in this section). Some evidence comes from coastal marine systems. Between 1951 and 1995, zooplankton biomass in coastal southern California waters decreased by 80% over four decades, at the same time the surface water layers warmed more than 1.5 °C in some areas. The surface warming appeared to result 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. Other research 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
Box 1  Selected references for current climate change impacts on biota


In general, the observations of most of these types of 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.

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 climate change, 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 face in the twenty-first century.

References


