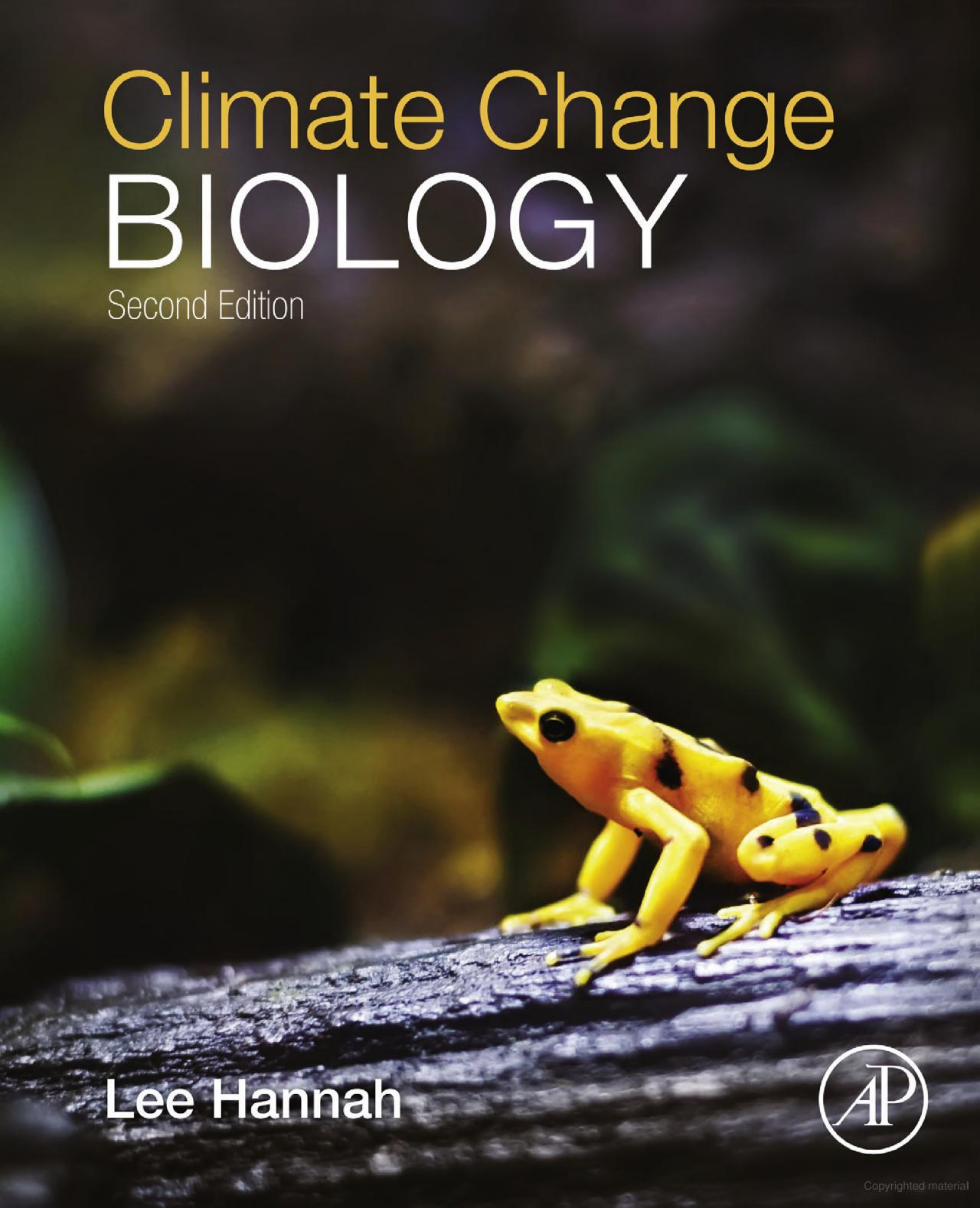

Climate Change
BIOLOGY

Second Edition

Lee Hannah

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USING THE FIGURES

The figures and boxes in this book are designed to provide a window into the primary literature. Many of the figures and all of the ‘spotlight’ boxes have been selected to represent classic climate change biology references. The sources for those figures and boxes are given in *author, date* format in the caption or at the end of the box, with the citations given in the reference list at the end of the book. More detailed explanations of many of the figures are available at http://booksite.elsevier.com/9780124202184. Instructors can assign readings from the primary literature to help build understanding of how a field evolves from primary research. Interested students can use the figure references and online explanations as access points to the peer review literature for research assignments or deeper understanding of concepts discussed in the text.

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1

SECTION

Introduction

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CHAPTER 1

A New Discipline: Climate Change Biology

The sun warms the Earth. Gases in the atmosphere capture heat and reradiate it back to the surface. This "greenhouse effect" transforms the Earth from a cold, rocky ball into a living planet. But how does this system operate, and how are human actions affecting this natural process?

These questions have been largely ignored in biology and conservation in the past. The recognition that human change is occurring in the climate—and that natural change is inevitable—is leading to a revolution in biology. A new discipline is emerging, melding well-established fields of inquiry such as paleoecology with new insights from observations of unfolding upheaval in species and ecosystems. The scope of the discipline encompasses all of the effects of human greenhouse gas pollution on the natural world. This is climate change biology.

The changes are too big to ignore. Extinctions have begun, and many more are projected. Species are moving to track their preferred climates, the timing of biological events cued to climate is shifting, and new plant and animal associations are emerging, whereas well-established ones are disappearing. Biologists are seeing change everywhere, and nowhere is change more important than in dealing with climate.

Climate change biology is the study of the impact of climate change on natural systems, with emphasis on understanding the future impacts of human-induced climate change. To understand future change, the discipline draws on lessons from the past, currently observed changes, biological theory, and modeling. It encompasses many existing disciplines, including paleoecology, global change biology, biogeography, and climatology. Climate change biology uses insights from all of these disciplines but not all of the results of these disciplines. For instance, paleoecological data that help us understand how biological systems will respond to anthropogenic climate change are a major part of climate change biology, but many aspects of paleoecology may remain outside the realm of the new discipline. Climatology is relevant to climate change biology but most climate studies fall outside the discipline. However, when climatologists conduct studies specifically to unlock biological mysteries, climatology is part of climate change biology. The practitioners of climate change biology therefore

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come from a broad range of biological and physical sciences, and their inclusion within the discipline is defined by their interest in understanding biological responses to climate change, particularly future changes due to human influences on the Earth's atmosphere (Figure 1.1).

SPOTLIGHT: BIRTH OF A DISCIPLINE

Rob Peters and Thomas E. Lovejoy founded climate change biology when both were with the World Wildlife Fund in the late 1980s. Lovejoy famously met with Steve Schneider (then director of the National Center for Atmospheric Research) and said, "I want to talk about how what you do affects what I do." Lovejoy describes the ensuing discussion as an "aha" moment for both scientists. Peters took the "aha" idea and turned it into the discipline of conservation in the face of climate change. A great poker and street hockey player, Peters was no stranger to getting to the spot before others. His papers with various coauthors in the late 1980s and early 1990s outlined much of early thinking on the subject. They were the first in their field. The classic 1985 article, "The Greenhouse Effect and Nature Reserves," framed the issues to be confronted succinctly (Peters and Darling, 1985). It even opened with a passage from Shakespeare (Macbeth): "I look'd toward Birnam, and anon, methought, the wood began to move."

Peters, R.L., Darling, J.D.S., 1985. The greenhouse effect and nature reserves. BioScience 35, 707–717.

FIGURE 1.1 **Earth's atmosphere.**

The atmosphere of the Earth is an amazingly thin layer of gases. At its thickest, the atmosphere is approximately 100 km deep, which is less than 1/100 of the Earth's diameter (12,700 km). Viewed from this perspective, the atmosphere appears as a thin, vulnerable shroud around the Earth. Alterations to this gossamer protective layer may have major consequences for life. *Source: Reproduced with permission from NASA.*

Climate change biology explores the interactions of biological systems with the climate system, as well as the biological dynamics driven by climate change. The interactions are not small. The climate system is in many respects driven by biology. Atmosphere and climate are themselves the products of eons of biological processes. Biological by-products are the very gases that capture the warmth of the sun and transform the planet. Everything from the color of plants across vast areas to the cycling of moisture between plants and the atmosphere help determine climate. The cycle is completed as the interactions of climate with biology determine where plants and animals can live, in turn influencing where, how far, and how fast they will move.

A GREENHOUSE PLANET

Water vapor and carbon dioxide (CO_2) are the two most abundant greenhouse gases in the atmosphere. They are both transparent to visible light arriving from the sun, but each traps heat coming from the Earth's surface (Figure 1.2). Both occur naturally, but CO_2 is also released by human burning of fossil fuels. The increase in atmospheric CO_2 concentrations resulting from human pollution is projected to cause major alterations to the Earth's climate system and global mean temperature in the twenty-first century.

Evidence spanning millions of years, and particularly from the past million years, suggests that greenhouse gases are a critical component of the Earth's climate system. Warm periods have been repeatedly associated with high levels of atmospheric CO_2 during the ice ages of the past 2 million years. Deeper in time, periods of high CO_2 concentrations or methane release have been associated with global warm periods.

GREENHOUSE EFFECT

Some gases in the Earth's atmosphere "trap" heat. Sunlight warms the Earth's surface, which then radiates long-wave radiation. Some of this radiation is absorbed and reemitted by gases such as CO_2 and water vapor. Part of the reemitted radiation is directed back at the Earth, resulting in a net redirection of long-wave radiation from space and back to Earth. This warms the lower reaches of the atmosphere, much as glass in a greenhouse traps heat from the sun, and so is known as the greenhouse effect.

The concentration of CO_2 in the atmosphere increased more than 30% in the twentieth century. This increase is due primarily to the burning of fossil fuels. Beginning with coal at the outset of the industrial revolution, and transitioning to oil and natural gas as economies advanced, the power for our electricity, industry, and transport has been drawn heavily from fossil fuels. Fossil fuels

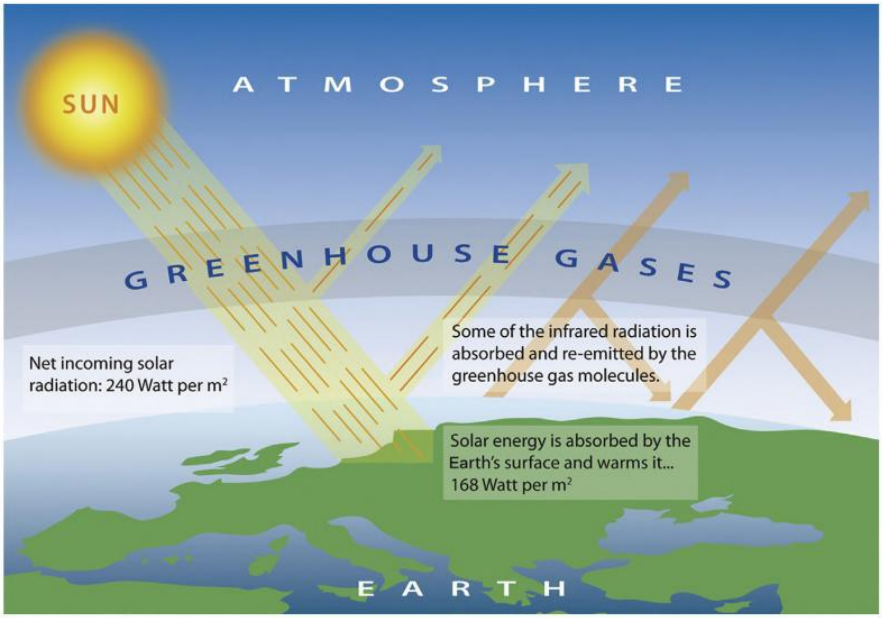

FIGURE 1.2 **The greenhouse effect.**
Solar radiation reaches the Earth, warming the surface. The surface then radiates long-wave radiation back toward space. Greenhouse gases absorb and reemit some of this long-wave radiation. The net effect is that some radiation that would have escaped to space is reradiated within the atmosphere, causing warming. *Source: From Climate Change 2001: The Scientific Basis. Intergovernmental Panel on Climate Change, 2001.*

are rich in carbon, and burning them both releases their stored energy and combines their carbon with oxygen to produce CO_2.

Rising CO_2 levels have direct effects on the growth of plants and on seawater chemistry while indirectly leading to global warming. These direct and indirect effects have profound implications for biological processes and the survival of species.

BOUNDARIES OF LIFE

Every species has climatic and physical tolerances that determine where it can live. Most species also initiate internal processes based on climatic cues. These two factors combine to determine much of the biology of how species interact, including how individual pairs of species share space and react to one another and how multiple-species assemblages come to exist together.

For example, coral reefs grow where the combination of water temperature and seawater chemistry falls within a relatively narrow range of suitable conditions. Water temperature must be above approximately 10 °C for reef-building, shallow-water corals to survive. At between 28 and 31 °C, depending on region and species, corals suffer high mortality. These same corals require dissolved calcium carbonate levels of 0.3Ω(Ω measures the degree of saturation of seawater with aragonite, a form of calcium carbonate) in order to produce their calcium carbonate skeletons and build reefs. Coral reefs are therefore found only in warm waters, primarily in the tropics, where seawater saturation with calcium carbonate is sufficient.

Species interactions with one another are often critical in mediating the effects of climate change. For example, the exact mechanism of coral mortality at high temperatures, is driven by a species interaction. Zooxanthellae are algae symbionts of corals that live within the coral polyp. These symbionts photosynthesize, nourishing the coral, while the coral provides a skeletal structure that keeps the zooxanthellae near the surface, where light for photosynthesis is abundant. At very high temperatures, the symbiosis breaks down and the coral expels the zooxanthellae. Without the photosynthetic pigments of their algal symbionts, the coral turns white or "bleaches." Some bleached corals regain their zooxanthellae and recover, but many die. Reef-building corals therefore have both thermal and ocean chemistry limits to their distribution, with species interactions, in this case in the form of symbiosis, determining the exact upper thermal limit of survival.

The combination of factors that determines where a species can survive is familiar to ecologists as the concept of niche. As with corals, most species respond directly to temperature or other climatic variables in both direct and indirect ways. Earlier definitions of niche, including those of Joseph Grinnell, who created the term in 1917, placed emphasis on species interactions as determinants of survival. Although some species interactions are nonclimatic, many others, such as the coral's interplay with zooxanthellae, are inextricably linked to climate. Later ecologists refined the concept, giving even greater emphasis to environmental variables. G. Evelyn Hutchinson defined the concept of niche as a composite (multidimensional hypervolume) of the environmental gradients across which a species could live. Many of the environmental variables relevant to this definition of niche are climatic, including temperature, precipitation, and rainfall seasonality. A polymath, Hutchinson also once said, "I sincerely hope that all of the things we are doing to the Earth's atmosphere cancel each other out."

Rapid, human-induced climate change is driving major movements in niche space. Thousands of range shifts have been recorded in plants, birds, mammals, amphibians, and insects. These range shifts result when climatic gradients shift as a consequence of global warming. Species' climatic tolerances do not change (or do not change as rapidly as climate is changing), so they must track suitable climate to survive. In today's landscapes heavily dominated by human uses such as agriculture and cities, tracking suitable climate can be a major problem for species.

In one of the earliest documented cases of shifting ranges, Edith's checkerspot butterfly was found to be shifting northwards and upslope. Similar shifts have now been found in hundreds of butterflies as well as many other invertebrates and many vertebrates such as birds and fish. Range shifts in plants are being recorded from the Cape of Good Hope in Africa to the Alps in Europe.

SHIFTING INTERACTIONS

As ranges shift, ecology is reinvented. The concept of community seems outmoded because species move in response to their own unique climatic tolerances, not as groups of organisms. Species that have coexisted throughout human memory turn out to be members of relatively ephemeral assemblages when viewed on geologic timescales.

For example, drought is driving the dieback of pinyon pines (*Pinus edulis*) across huge portions of the southwest United States. Pine dieback has affected more than 1,200,000 ha of pinyon–juniper woodland, making the pinyon–juniper association look temporary for much of the area it used to characterize. Referring to a pinyon–juniper "community" still has descriptive value because where it still exists, the association is home to many species in common. But for ecological purposes it has become clear that junipers and pinyons do not exist as an interdependent unit: They have simply shared similar climatic conditions within their respective tolerances, but those conditions are now diverging.

The same is true for species and their food. Switching of long-standing prey preferences or primary patterns of herbivory have now been seen owing to climate change in many areas. Edith's checkerspot butterfly populations in California's Sierra Nevada mountains have switched from feeding predominantly on blue-eyed Mary (*Collinsia parviflora*) to English plantain (*Plantago lanceolota*) owing to mismatching of caterpillar emergence and nectar availability due to climate change.

CHEMISTRY OF CHANGE

In the oceans and on land, greenhouse gas pollution also has direct effects on biological systems. CO_2 dissolves in seawater to produce acid and reduce the amount of calcium carbonate held in the water (saturation state). Reduced saturation state makes it more difficult or impossible for creatures to secrete calcium carbonate shells or skeletons. Consequences may include extinction, reduced abundance, or range shifts for species as diverse as squid, shelled sea creatures, and corals. Acidification can have direct effects by altering the pH of seawater. Ocean surface waters already have about 30% more H^1 ions (less basic; pH change from 8.1 to 8.0) due to dissolving of CO_2 pollution during the past two centuries (Figure 1.3).

FIGURE 1.3 **Ocean chemistry and marine life.**
Marine organisms such as these Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are already experiencing ocean acidification. The pH of seawater varies significantly by region and by depth, and it is increasing owing to human CO_2 emissions. CO_2 from human fossil fuel combustion enters the atmosphere and then dissolves in seawater, making it more acidic. Surface waters already contain about 30% more hydrogen ions than they did in preindustrial times. *Source: Courtesy of NOAA.*

On land, CO_2 stimulates plant growth because it is one of the principle inputs to photosynthetic pathways. This effect is not uniform for all species, and it may favor plants using the C_3 photosynthetic pathway. Global vegetation patterns may therefore be influenced by direct CO_2 effects as well as by warming. The complex, long-term effects of CO_2, either in the oceans or on land, are yet to be fully understood.

LINKAGES BACK TO CLIMATE

Biological systems have thermal properties and emit gases that in turn change climate. The amount of the sun's energy reflected (albedo) or absorbed changes greatly when vegetation changes. The replacement of tundra with coniferous forest owing to climate warming is darkening boreal latitudes, increasing heat absorption and causing further warming. The moisture transpired by trees in one area of the Amazon condenses in the atmosphere and falls as rain in other areas of the Amazon. Conversion of rain forest to savanna breaks this cycle and can lead to descent into mega-drought. The climate system is therefore influenced by what happens to biological systems, completing the chain of causation.

Natural CO_2 fluxes are large relative to emissions from fossil fuel burning, but the human emissions are enough to disturb the natural balance of the carbon cycle and increase atmospheric concentrations. How much and how fast they increase depends in large part on what is happening in other parts of the (natural) carbon cycle. Understanding the sinks, sources, and fluxes of the carbon cycle is a priority for understanding the full linkages between climate and biology.

CLIMATE CHANGE BIOLOGY

Climate change biology is a field of growing interest to a new generation of biologists, conservationists, students, and researchers. Understanding the impacts of greenhouse gases on biology and understanding the influence of biology on climate are in their infancy. The body of knowledge of past change is large, however, and the chronicle of changes currently under way is substantial and rapidly growing.

Progress in the field will help us understand how organisms respond to climate change, what conservation measures can be designed to lessen the damage, and how the interplay between the biosphere and the climate will determine the health of human and natural systems for centuries to come. The outcomes for nature are not divorced and separate from human health and happiness but, rather, are integral to achieving long-term human development in the face of climate change. Human development depends on healthy natural systems. People increasingly turn to nature for inspiration and to the outdoors for recreation, as well as relying on myriad natural systems for provision of food and materials. Maintaining healthy natural systems is an immense challenge when those systems change rapidly, as they are today.

Exploring what we have learned so far sets the stage for fuller understanding. Principles are emerging, such as the ephemeral nature of communities, that will provide a solid foundation for learning in the future. There will certainly be surprises—we are putting the planet through the largest, fastest climatic change since the rise of human civilization—but the early identification of, and learning from, those surprises is part of the excitement of a new field of inquiry. Management responses will at first be based on current fragmentary understanding, but with time, management lessons will emerge and help refine the science underpinning our early assumptions.

The structure of this book follows these principles. An overview of the climate system concludes this introductory section. The second section explores the impacts of human-induced climate change on nature that are currently being observed. The third section turns to the past for lessons about climate change in terrestrial, marine, and freshwater biological systems. Based on these insights, theory and modeling of future potential change are explored in Section 4. The last two sections of the book explore how the insights of climate change biology can be applied to the design of more dynamic conservation systems and how international policy and greenhouse gas reduction efforts influence biology and conservation.

Training the next generation of climate change biologists begins now. The first generation of climate change biologists were generally researchers specialized in other areas of ecology or biology, either finding new relevance for their observations or discovering the importance of climate change to their field of inquiry. The next generation will often be interested first in climate change and then in the tools of other subdisciplines as a means of exploring climate change questions. As it takes its place in more established circles, climate change biology is ready to provide answers of immense importance to people and nature, for generations to come.

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CHAPTER 2

The Climate System and Climate Change

This chapter introduces the basics of the climate system and climate change. How do we know climate is changing? How are future changes simulated? What causes natural and anthropogenic climate change? These questions are answered here, forming a foundation for climate change understanding that is needed to explore biological responses.

THE CLIMATE SYSTEM

The Earth's climate system is composed of the atmosphere, the oceans, and the Earth's land surface (Figure 2.1). The dynamic elements of the system are hydrology and the movement of gases, including water vapor. Elements external to the climate system but very important in determining its behavior include the sun, variations in the Earth's orbit in relation to the sun, and the shape and position of continents and oceans.

The atmosphere traps energy by capturing and reradiating radiation that would otherwise escape into space. Long-wave radiation (heat) given off by the land surface and oceans is absorbed by greenhouse gases in the atmosphere. This energy is then reradiated in all directions, the net effect being a trapping of a portion of the energy in the Earth's atmosphere near the surface. Clouds in the atmosphere can reflect incoming solar energy, cooling the surface. During the day, this effect can outstrip the warming effect of the water vapor in the clouds, whereas at night the warming effect of clouds dominates. The main constituents of the atmosphere are nitrogen (78%) and oxygen (21%). Water vapor and CO_2 are minor constituents of the atmosphere but potent greenhouse gases.

The oceans are the second major component of the climate system. From a climatic standpoint, the greatest importance of the oceans is as vast reservoirs of water and dissolved gas. The oceans contribute most of the water vapor found in the atmosphere. Warmer oceans give off more water vapor. They also produce larger and more severe storms such as hurricanes. The oceans absorb CO_2, reducing its concentration in the atmosphere.

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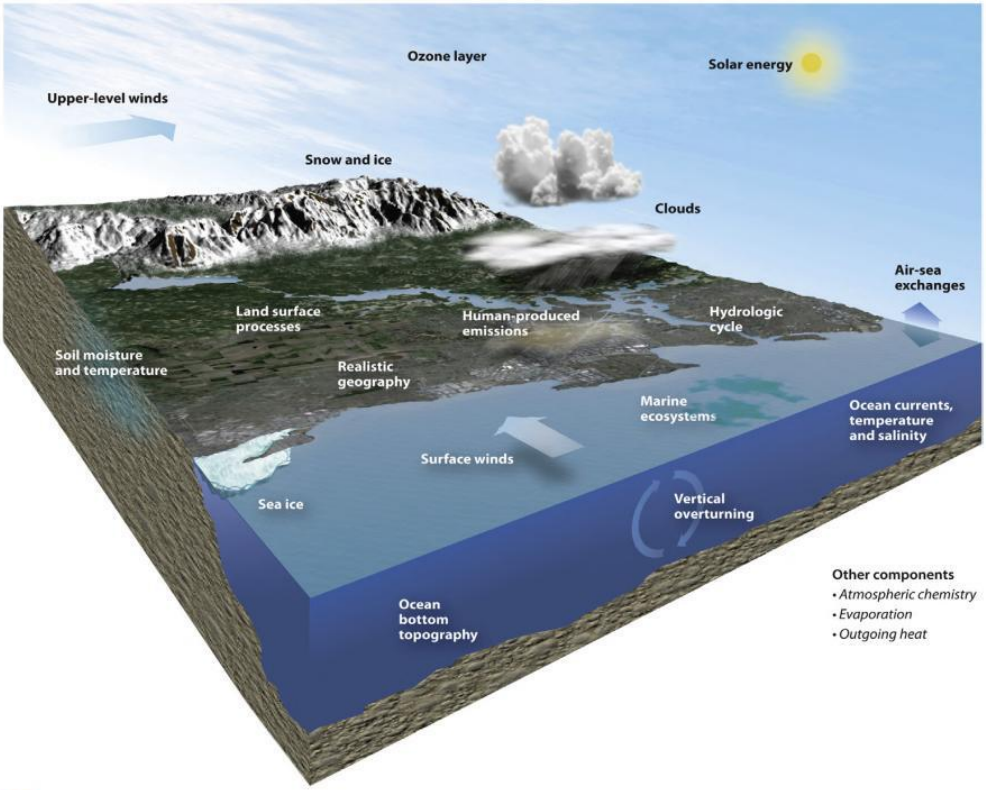


FIGURE 2.1 **Climate system elements.**
The land surface, oceans, and atmosphere are the major elements of the climate system. Human-driven change in the climate system acts largely through additions of greenhouse gases to the atmosphere. *Copyright UCAR, reproduced with permission of UCAR/NCAR.*

The land surface consists of vegetation, exposed soil and rock, human structures, and snow and ice. The reflective properties of these surfaces make a large difference in how the planet warms. Dark surfaces absorb solar energy and reradiate it as heat that may be trapped by greenhouse gases in the atmosphere. Light surfaces reflect sunlight back into space in wavelengths not trapped by greenhouse gases, so they have a cooling effect.

Snow and ice are particularly important parts of the Earth's surface in the climate system because they reflect the sun well. White surfaces reflect solar energy, cooling the Earth's surface. Glaciers, snowpack, and sea ice all measurably cool the Earth by reflecting sunlight. Increases in average global temperature reduce the area of ice and snow by melting, thus reducing the resultant reflectivity of the planet and producing a positive feedback loop in the climate system as the Earth warms still further (Figures 2.2–2.4).

POSITIVE FEEDBACKS IN CLIMATE

There is a positive feedback on warming when snow and ice melt. Snow and ice reflect light. Their reflectance is measured as the albedo. Light-colored materials have a high albedo, and dark materials have a low albedo. The near white of snow and ice gives them a high albedo, whereas the dark waters revealed when ice melts or the dark needles of forest conifers revealed when snow melts have a low albedo. This means that water or forest absorbs more energy from sunlight than does snow or ice, accelerating warming.

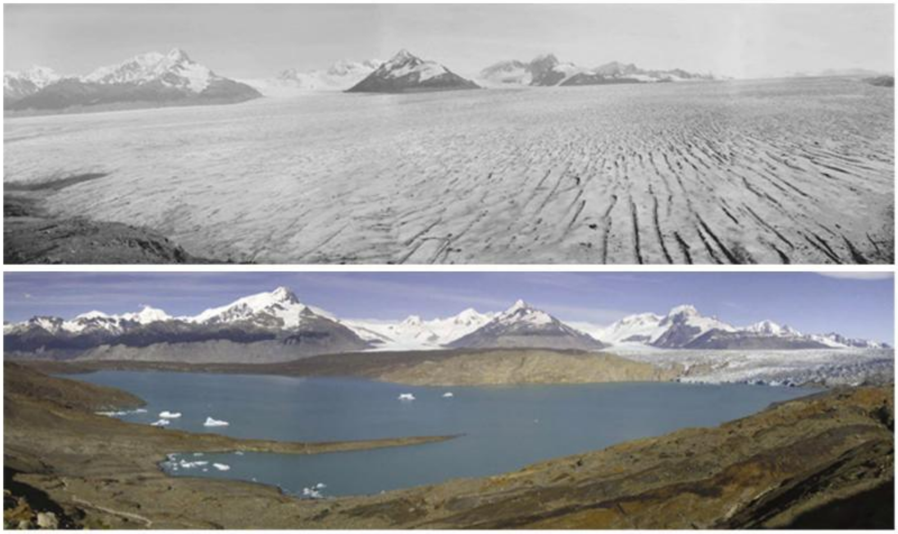


FIGURE 2.2 **Upsala glacier, patagonia, 1928 (top) and 2004 (bottom).**
Source: Top: © Archivo Museo Salesiano/De Agostini. Bottom: © Greenpeace/Daniel Beltrán.

Hydrology is the movement of water within and between elements of the climate system. Because water vapor has powerful heating (greenhouse gas) and cooling (daytime clouds) effects, the movement of water is of unparalleled importance in the climate system. Water moves through the hydrologic cycle, evaporating from the oceans, condensing as clouds, and then raining out over land to form fresh water that flows to the sea. Increases in global temperature can accelerate this hydrologic cycle by speeding up evaporation from the ocean surface.

EVOLUTION OF THE EARTH'S CLIMATE

The atmosphere as we know it was made possible by life. The atmosphere, in turn, made higher life-forms possible. The Earth was formed 4.5 billion years ago, and within approximately 1 billion years single-celled life appeared. Microbial photosynthesis over hundreds of millions of years produced enough

FIGURE 2.3 Boulder glacier, glacier national park, 1932.
Source: Reproduced with permission from Archives and Special Collections, Mansfield Library, The University of Montana.

FIGURE 2.4 Boulder glacier, 1988.
Source: Reproduced with permission from Archives and Special Collections, Mansfield Library, The University of Montana.

oxygen to make it a major component of the atmosphere. Much of this photosynthesis occurred in microbial mats, some of which formed structures known as stromatolites, which are stony accretions that are dominant in the fossil record for billions of years. By approximately 600 million years ago, oxygen buildup was sufficient to support the formation of an ozone layer in the upper atmosphere. Sunlight bombarding the upper atmosphere split oxygen atoms to create free oxygen radicals, some of which recombined with oxygen to form ozone. At this point, even though atmospheric oxygen levels were still only a fraction of modern levels, the major characteristics of modern atmosphere were in existence—oxygen, nitrogen, water vapor, and an ozone layer.

The ozone layer allowed terrestrial life to emerge. Previously, life had been possible only in the oceans, where the water column shielded organisms from damaging UV radiation. With the emergence of the ozone layer, UV radiation was screened out in the upper atmosphere, allowing life-forms to emerge onto land. Photosynthetic organisms were still dominant, allowing the continuing buildup of oxygen in the atmosphere.

The interaction of the atmosphere, water, and continental configurations began to govern climate. Major changes in climate were associated with the periodic formation of supercontinents, glacial episodes, and volcanism. At least three supercontinents have existed in the past billion years of Earth history. Rodinia existed from approximately 1 billion years ago to 750 million years ago. Pannotia was formed approximately 600 million years ago and lasted for 50–60 million years. The most recent supercontinent, Pangaea, was formed approximately 250 million years ago and later broke into its constituent components of Gondwanaland and Laurasia. Among several episodes of volcanism, the greatest was the massive outpouring that formed the Siberian Traps 250 million years ago.

The Earth's climate alternated between "icehouse" and "greenhouse" conditions once the modern atmosphere had evolved. Major icehouse episodes in deep time occurred between 800 and 600 million years ago and again at about 300 million years ago. The Earth has generally been warmer than in the present since emerging from icehouse conditions approximately 280 million years ago, but there have been remarkable increases and decreases in temperature within that time span as well.

There have been four major warm periods and four major cool or cold periods during the past 500 million years (Figure 2.5). During cool or cold phases, there is polar ice and substantial ice on land, and the global mean temperature is low. In the warm periods, there is little or no polar ice or ice on land. The warm periods generally are associated with high atmospheric CO_2 levels, whereas the icehouse periods are associated with low CO_2. Warm greenhouse conditions dominated for most of deep time (100 million to 1 billion years ago) but were punctuated by several icehouse episodes. More recently,

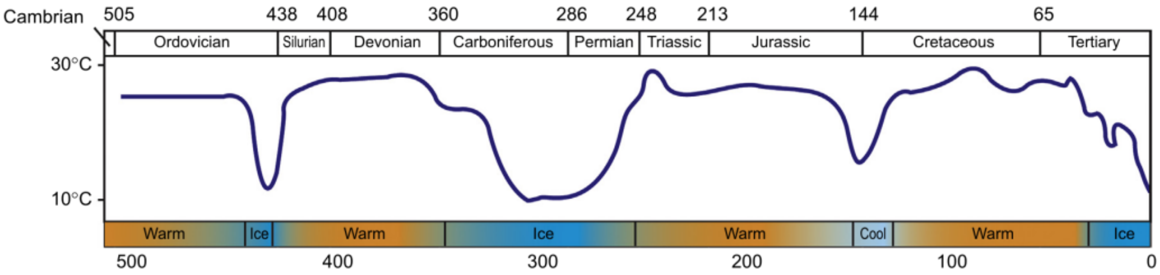


FIGURE 2.5 **Global temperature during the past 500 million years.**
Global mean temperature has fluctuated between icehouse and hothouse conditions during the past billion years. Four major hothouse periods have seen a largely ice-free planet, whereas four major icehouse periods have had major polar or continental ice sheets. The current climate is in a warm phase within an icehouse period. *Source: Reproduced and redrawn with permission from Christopher R. Scotese.*

a gradual cooling has dominated, leading to the ice ages of the past 2 million years. The current 10,000-year interglacial period is one of several brief warm blips in the predominantly icehouse conditions of the past 2 million years.

During the past 100 million years, a slight cooling trend gradually reversed approximately 80 million years ago and then was interrupted by a dramatic, brief warm period approximately 55 million years ago (Figure 2.6). During this warm spike, global mean temperature rose several degrees very rapidly and then dropped again only a few million years later. This spike, known as the Paleocene-Eocene Thermal Maximum (PETM), was followed by gradual warming that led to a longer warm period known as the Early Eocene Climatic Optimum.

Cooling dominated from 50 to 30 million years ago, leading to ice formation in both the northern and the southern polar regions approximately 40 million years ago. This ice cover was sporadic at first and then became continuous in Antarctica in a rapid cooling event approximately 34 million years ago. Slight warming kept the ice cover in the Northern Hemisphere sporadic until approximately 2 million years ago, when the Pleistocene ice ages began.

Climate dynamics have been particularly pronounced during the past 2 million years as the Earth has plunged into, and more briefly back out of, glacial periods (see Fig. 2.6). Glacial conditions have dominated this period, with warm greenhouse intervals coming at roughly 100,000-year intervals and lasting only a few thousand years each. This period has been characterized by much climatic variability, including very rapid climate “flickers”—sudden shifts to warmer or colder conditions that occurred in less than 1000 years.

Glacial/interglacial transitions are driven by orbital forcing of climate. When conditions are right for land ice to last through many summers in the large landmasses of the Northern Hemisphere, an ice age is initiated. As solar input

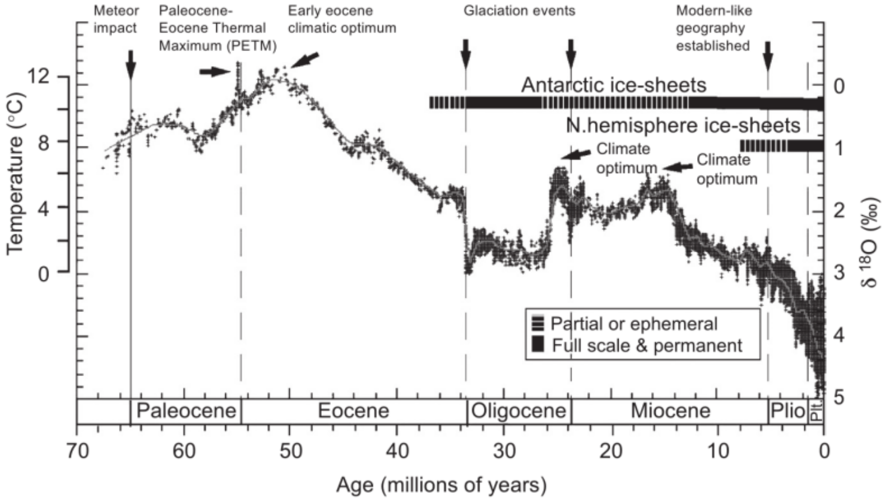


FIGURE 2.6 **Earth temperature change during the past 70 million years.**
The past 70 million years have seen the planet cool from the thermal maximum at the Paleocene–Eocene boundary 54 million years ago to current ice age conditions. Polar ice formed in the Southern Hemisphere beginning approximately 35 million years ago and in the Northern Hemisphere approximately 8 million years ago. Northern Hemisphere polar ice became permanent approximately 2 million years ago, initiating the ice ages. *Source: Zachos et al. (2001) Reprinted with permission from AAAS.*

to northern landmasses changes with variations in the Earth's orbit, the northern land ice melts, initiating a warm, greenhouse interval.

The last glacial period gave way to the current warm period starting approximately 10,000 years ago (the Holocene). After several late-glacial climate flickers, notably the Younger Dryas, the climate became more stable as recorded in Greenland and Antarctic ice cores, though pollen records suggest substantial climate variation in both temperate and tropical areas. Orbital forcings are unusual in this period and may result in an interglacial period considerably longer than those typical of the past 500,000 years. It is onto this unusually warm, stable climate that human greenhouse gas emissions are pushing additional climatic warming.

NATURAL DRIVERS OF CHANGE

Energy from the sun drives the climate system. The sun's warmth is unevenly distributed across the planet, which sets winds and ocean currents in motion, transporting heat from the equator to the relatively cooler poles. Energy from the sun drives the hydrologic cycle as well, evaporating water from the oceans and freshwater bodies. Natural forcings such as volcanic eruptions modify summer climate on shorter timescales (Figures 2.7 and 2.8).

SPOTLIGHT: FORCING THE SYSTEM

The climate system is forced by both natural and human-driven processes. Orbital forcing is particularly important in driving natural change. It includes variations in the Earth's orbit that result in relatively more or less solar radiation reaching the Earth. The Earth's orbit is not perfectly round; the tilt of the Earth on its axis varies in its orientation to the sun, and the tilt itself wobbles—it changes with time. All of these factors result in changes in incoming solar energy and drive changes in the climate system. Volcanic activity ejects large amounts of particulates into the atmosphere, causing cooling, and is another forcing external to the climate system (Figures 2.7 and 2.8). Finally, most recently and most dramatically, human pollution of the atmosphere with greenhouse gases has resulted in radiative forcing of the climate system—changes that affect the reradiation of the energy of the sun, warms the atmosphere and results in climate surprises.

Source: Schneider, S. H., 2004. Abrupt non-linear climate change, irreversibility and surprise. Global Environmental Change, 14 (3), 245–258.

FIGURE 2.7 Pinatubo eruption.

The summit caldera on August 1, 1991, a month and a half after the June 15 explosive eruption that ejected so much ash into the atmosphere that it altered global climate. *Photo by T. J. Casadevall, U.S. Geological Survey.* From http://www.beringia.com/climate/content/volcanoes.shtml.

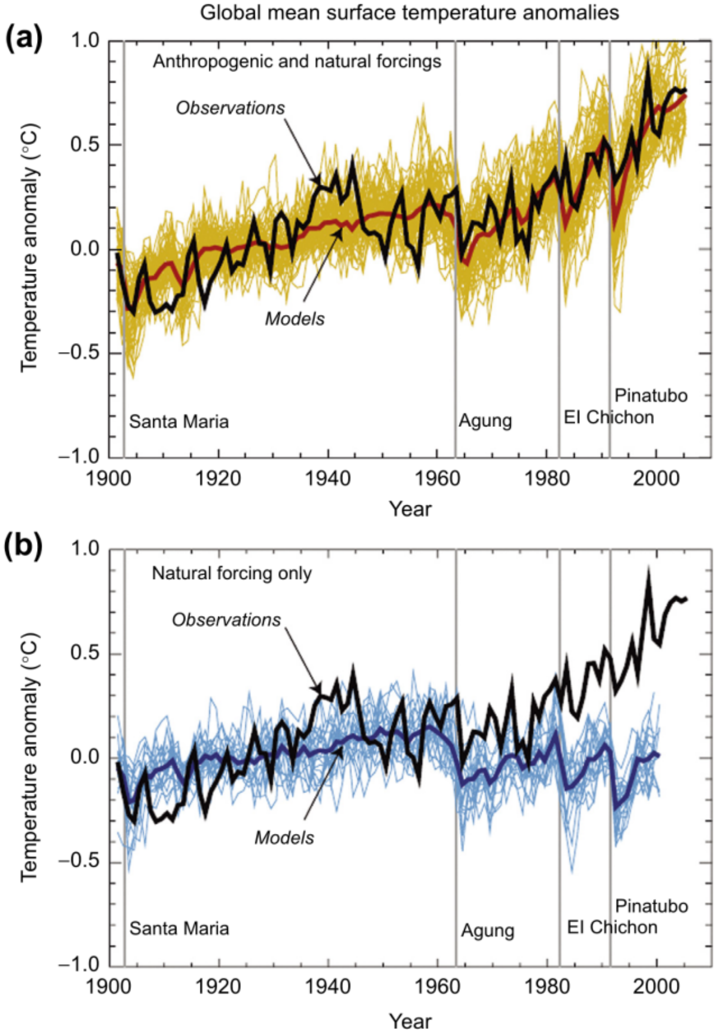


FIGURE 2.8 Global temperature change due to natural and human forcing.
Global temperature cooled measurably in the years immediately after the Mount Pinatubo eruption (bold line). This global temperature trace indicates major volcanic events that drove decreases in global temperature. It is coupled with mean temperature projections from global climate models (general circulation model—GCM), computer simulations (colored lines) showing that the actual temperature record can be fully reproduced only when human forcings, primarily burning of fossil fuels and deforestation, are included in the GCM simulations. *Source: From Climate Change (2007): The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Figure TS.23. Cambridge University Press.*

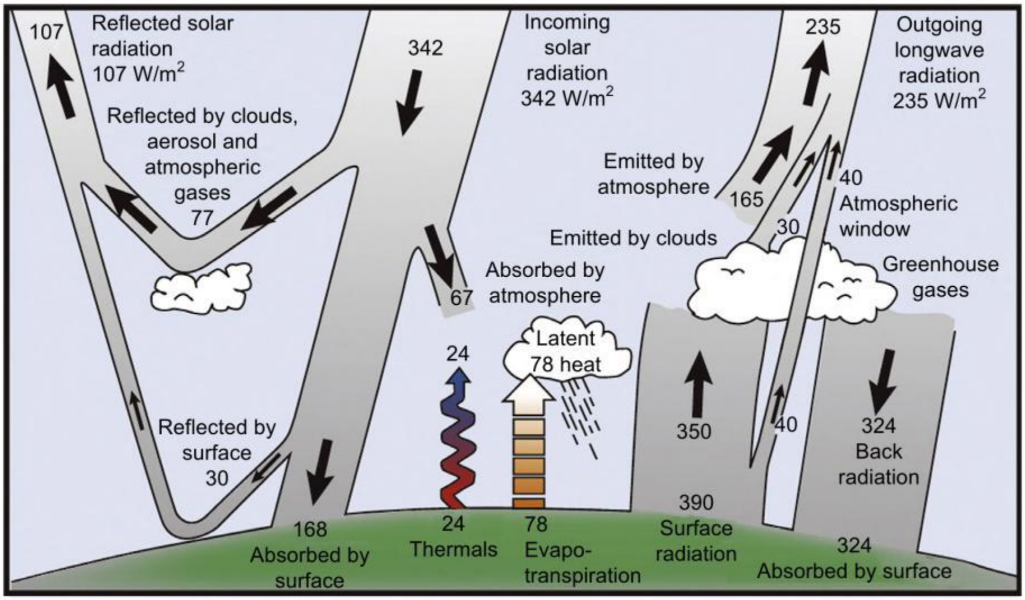


FIGURE 2.9 **Earth's radiation balance.**

Approximately 342 W/m^2 of solar energy reaches the Earth's surface. 107 W/m^2 is reflected into space, whereas 235 W/m^2 is emitted from the Earth as long-wave radiation. *Source: From Climate Change (2007): The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.*

The energy reaching the top of the Earth's atmosphere is estimated to average 342 W per square meter (W/m^2). Some of that energy is reflected back into space by fine particles in the atmosphere, clouds, or the Earth's surface, leaving approximately 235 W/m^2 to warm the atmosphere and the surface of the Earth (Figure 2.9). Over the whole Earth, this is an immense amount of energy—approximately 150 million times more energy than is produced by the world's largest power station.

The exact amount of energy reaching the Earth varies, however, as does the distribution of that energy to various parts of the world. Changes in the orbit of the Earth bring it closer to the sun or farther away or tilt one part of the planet closer to the sun. The energy output of the sun may vary as well, up to several tenths of 1%. These variations in orbit affect the amount of energy reaching the Earth, changing the sun's warming effect and hence changing climate.

There are three main types of orbital variation affecting the Earth's climate (Figure 2.10). The first, called eccentricity, relates to the shape of the Earth's orbit around the sun. The path that the Earth carves in space varies from nearly circular to strongly egg shaped (elliptical). When the orbit is elliptical,

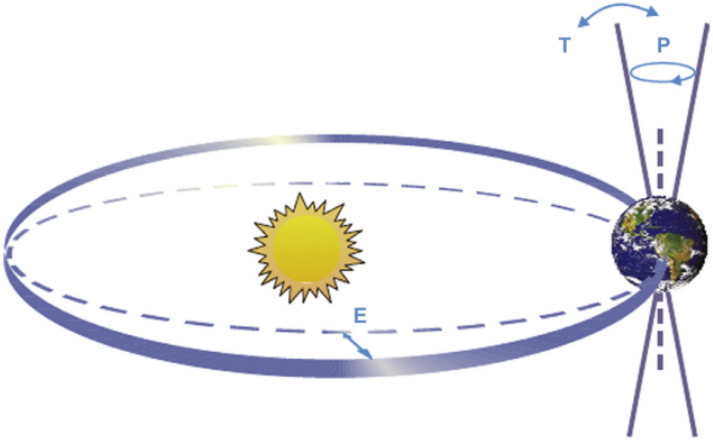


FIGURE 2.10 **Orbital forcings.**
Three major orbital forcings affect the amount of solar radiation incident on Earth. The Earth's orbit is oval rather than round, resulting in more radiation reaching the Earth when it is closer to the sun. This effect is eccentricity (E). The tilt of the Earth (T; also referred to as obliquity) varies, which affects the amount of radiation reaching the Northern Hemisphere. Finally, the time of year during which the Northern Hemisphere is tilted toward the sun varies, which is called precession of the equinoxes (P). These forcings are often referred to as Milankovitch forcings, for the Serbian physicist who recognized that the amount of solar radiation received in summer in the Northern Hemisphere determined the timing of ice ages. *Source: From Climate Change (2007): The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.*

the Earth will be much closer to the sun in some parts of its orbit, changing seasonal heating. The Earth wobbles on its axis as it circles the sun, giving rise to the second and third types of orbital forcing. The amount of tilt varies and is referred to as obliquity. The direction of tilt slowly rotates and is called precession.

All three of these orbital forcings affect the distribution of heating between seasons or between hemispheres more strongly than they affect the overall amount of solar energy reaching the Earth. Their effect on climate is therefore due to amplifications and dynamic effects rather than to changes in raw energy input.

The most pronounced of these amplifications are the ice ages, which are driven by the unequal amounts of land in the Northern and Southern Hemispheres. North America and Eurasia have huge landmasses near the poles. When the Northern Hemisphere receives less heat, particularly in summer, ice may form on this land. The ice reflects sunlight and cools the entire planet. When the Northern Hemisphere receives more heat, the ice melts and the planet warms. Warming and cooling of the Southern Hemisphere has no such effect because of the lack of land near the poles. There is very little land near the poles in South America and Africa because both taper as they approach the South Pole.

Precession determines which hemisphere tilts toward the sun in summer. Precession varies on a 23,000-year cycle. When the Northern Hemisphere is tilted toward the sun in summer, summers are very hot and ice cannot build up on the large northern landmasses.

Obliquity is the amount of tilt in the Earth's axis. The Earth wobbles on its axis like a spinning top. When the tilt is strong toward the Northern Hemisphere, it is difficult for continental ice sheets to form. There is a 41,000-year periodicity to obliquity. Obliquity is sometimes referred to as tilt.

Eccentricity is the shape of the Earth's orbit around the sun. This shape varies from more circular to more oval with two cyclic periods—100,000 and 400,000 years. The more circular orbit results in more even distribution of solar energy. The more oval orbit can result in less solar energy reaching the Northern Hemisphere's large, ice-prone landmasses and can help trigger a glacial period.

Glacial periods start with cool summers. Combinations of orbital forcings that lead to cool summers allow ice to be retained through the warm season and continental ice sheets to form in North America and Europe. The Northern Hemisphere landmasses are particularly important because they offer enough high-latitude landmass for the formation of continental ice sheets. A similar dynamic for the Southern Hemisphere does not exist because there is little landmass to hold ice in South America or Africa at high latitudes. In the late 1800s, scientists believed that cold winters led to ice ages. Milutin Milankovitch, a Serbian geophysicist and engineer, recognized that cool summers were the key to ice buildup. Cycles in orbital forcing—Milankovitch cycles—bear his name in recognition of his contribution to understanding their role in the ice ages.

Recent research points to a role for the Southern Hemisphere in the formation and termination of glacial periods as well, also driven by Milankovitch forcings. Low obliquity (tilt) brings cool summers to both hemispheres, which favors ice buildup in the north and intensified circumpolar current in the south. The intensification of the circumpolar current reduces upwelling of CO_2-rich water. The reduction in atmospheric CO_2 cools the planet, facilitating continental ice sheet buildup in the north. The Southern Hemisphere may also push the Northern Hemisphere along as glacial periods end—high obliquity results in warmer summers in both hemispheres. This begins to melt the continental ice sheets in the north, whereas in the south it intensifies circumpolar currents and winds, pumping CO_2-rich water to the surface and warming the planet.

MAJOR FEATURES OF PRESENT CLIMATE

Energy from the sun drives circulation patterns in both the oceans and the atmosphere. Atmospheric circulation is driven by the principle that warm air is less dense than cool air and therefore rises. Ocean circulation is driven by both temperature and salinity. Warm water rises, cool water sinks, and salty water is more dense than fresh water, leading salty water to sink and less salty water to rise.

The Earth receives more heat from the sun at the equator than it does at the poles. A pot that is off center on the stove also receives heat unequally, resulting in water roiling to the top where the heat is received and moving out to the cooler edges of the pot. The sun's heat received at the Earth's equator acts in the same way, causing the Earth's atmosphere to roil—warm air rises and builds up in the tropics, pushing toward the cooler poles. As air masses move from the tropics toward the poles, they cool, descend, and eventually return to the tropics in a giant loop. This movement of heat, known as heat transport, creates large, systematic patterns of circulation in the atmosphere.

This heat imbalance sets up gradients that drive heat transfer from the equator toward the poles. Warm air and water rise, pooling at the equator, setting up circulation patterns typified by rising warm air or water near the equator and sinking cold air or water near the poles, with movement in between.

In the atmosphere, these circulation patterns are known as Hadley cells (Figure 2.11). There are two Hadley cells between the equator and each pole. Hadley cells have both vertical and horizontal structures. Viewed in cross-section, air masses in a Hadley cell rise at the equator, move toward the pole, and then descend. From above, the circulation is clockwise, as moving air is deflected by the Coriolis effect imparted by the Earth's rotation.

In counterpoint to the Hadley cells, in the tropics there are East–West-oriented circulation cells. These circulation patterns arise when pressure differences across ocean basins drive surface winds in one direction, balanced by transfers aloft in the opposite direction. Over the Pacific Ocean, the circulation is known as Walker cell circulation or the "Southern Oscillation." It drives easterly surface winds across the Pacific. Breakdown in Walker cell circulation in the tropical Pacific results in an El Niño event.

Trade winds are surface winds caused by air movement and Hadley cells being deflected by the Coriolis effect. The trade winds are easterly, meaning that they blow from the east. They move westward along the equator in both the Northern and the Southern Hemisphere. Where the trade winds converge along the equator, a zone of uplift and cloud formation results, which is known as the Intertropical Convergence Zone (ITCZ). The trade winds are balanced by return flows in the midlatitudes by west-to-east blowing winds known as the westerlies.

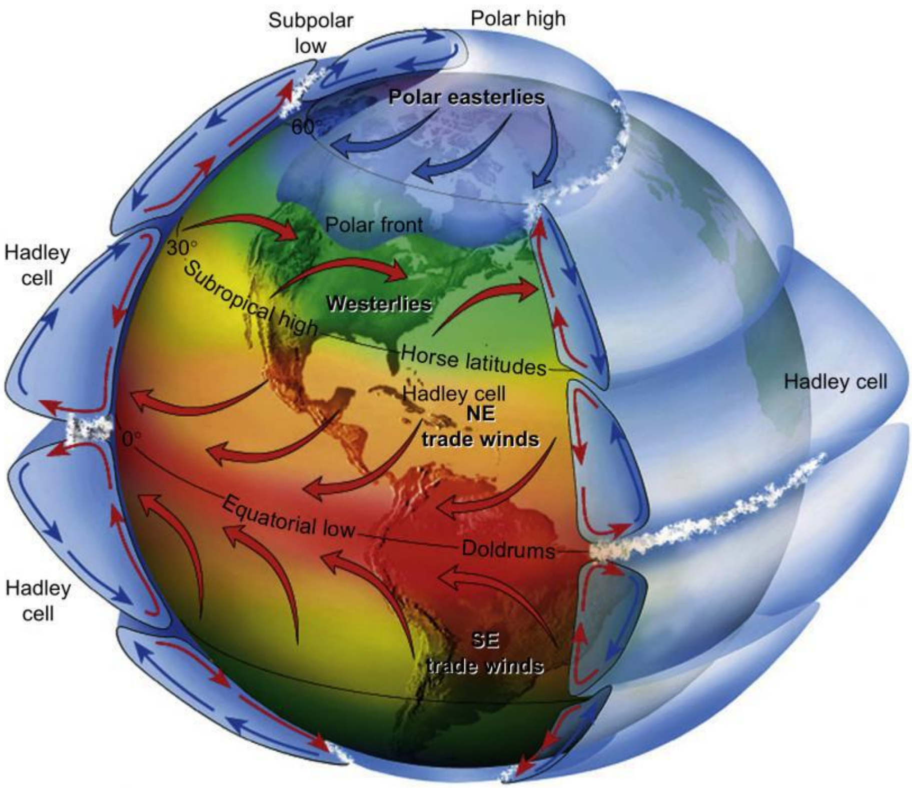


FIGURE 2.11 **Hadley cells.**

Warm air rises in the atmosphere, cools, and descends. This phenomenon results in the formation of major vertical circulation features in the atmosphere known as Hadley cells. Clouds form in the tropics where Hadley cells meet near the equatorial low - the Intertropical Convergence Zone (ITCZ). The ITCZ migrates north and south, resulting in two rainfall peaks in most parts of the tropics. *Source: Lutgens et al. (2001). Reproduced with permission from Pearson Publishers.*

Major ocean circulation patterns follow the wind patterns, forming large gyres with east-to-west flow along the equator and west-to-east flow at the midlatitudes. However, ocean current direction varies from wind direction by 15–45° progressively with depth, an effect known as the Ekman spiral. When surface ocean currents strike continents, they deflect and follow the shoreline, forming boundary currents.

Upwelling results when along-shore winds move ocean water. The wind-driven surface movement is deflected by the Ekman spiral, resulting in transport of water away from the coast. This moving water has to be replaced, so water from depth is drawn to the surface. The movement of this cold, nutrient-rich water from depth to the surface is referred to as upwelling (Figure 2.12).

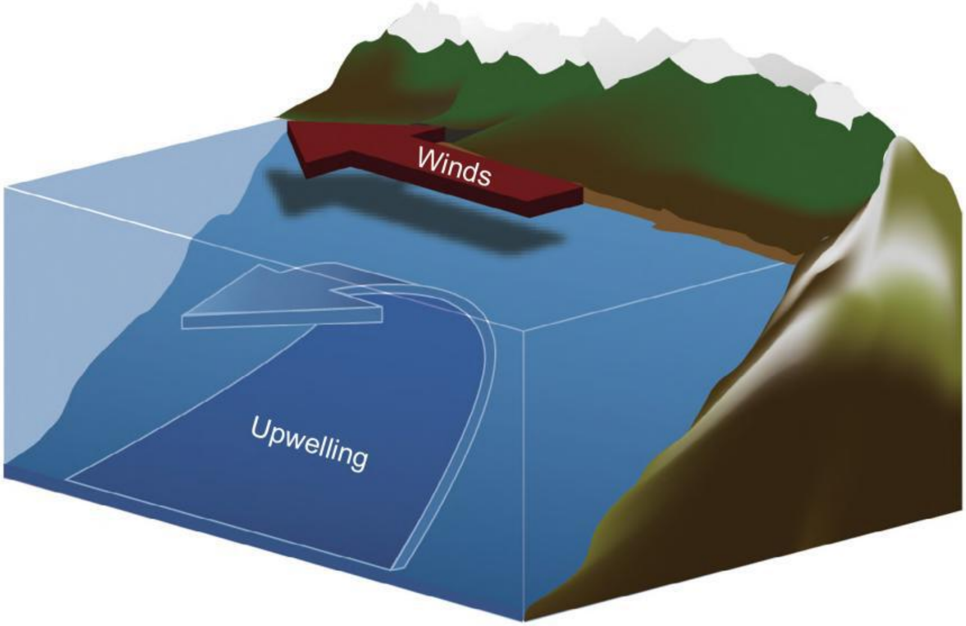


FIGURE 2.12 **Forces driving upwelling.**
Alongshore winds create water movement that is deflected by Eckman forces. Replacement water rises from the depths, creating upwelling. *Source: From Wikimedia Commons.*

In the oceans, the equator-to-pole circulation is the thermohaline circulation (Figure 2.13). It is more complex because it must work its way around landmasses and because it involves salinity as well as warmth. Warm water at the equator evaporates, leaving behind water that is both warmer and more salty, and hence more dense. This salty warm water moves toward the poles, where it cools and sinks, renewing the circulation.

The influence of the thermohaline circulation is especially strong in the North Atlantic, bringing in massive quantities of heat from the equator. This portion of the thermohaline circulation is known as the Gulf Stream. When the Gulf Stream shuts off, it robs heat from two major landmasses near the poles, greatly accelerating ice buildup. Glacial periods seem to end when the Gulf Stream strengthens, pumping energy northward to melt the ice sheets. Whereas the onset of glacial periods seems to be more gradual, the end of a glacial period can be dramatically rapid. Climate flickers such as the Younger Dryas can be initiated when the thermohaline circulation shuts down during the glacial/interglacial transition. Changes in the thermohaline circulation are therefore an important trigger for climate change.

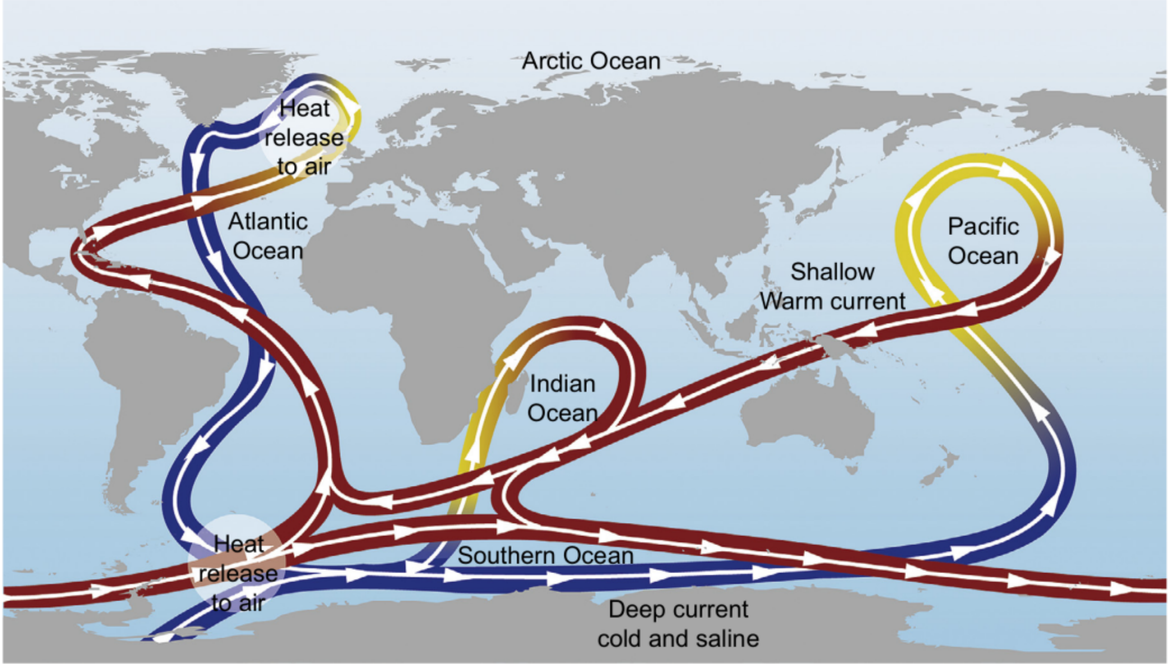


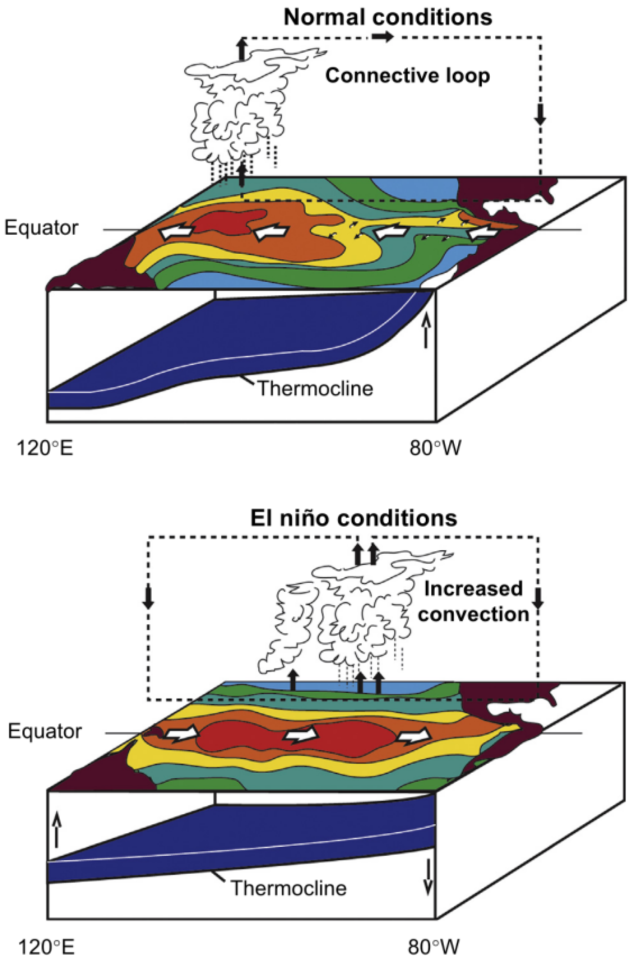
FIGURE 2.13 **Thermohaline circulation.**

Major circulation features in the oceans are established when seawater warms at the equator, evaporating and becoming more saline, and then moves near the surface (red) toward the poles, where it cools and sinks. It then moves near the bottom (blue) back to the equator, to rise and begin the process anew on timescales of hundreds of years. Because it involves both temperature and salinity, this feature is termed thermohaline circulation. *Source: Lovejoy and Hannah (2005). Reproduced with permission from Yale University Press.*

STABLE STATES OF THE SYSTEM

The circulation patterns of the Earth's climate system change over time. Like freeway traffic that either moves freely or backs up clear across town, atmospheric circulation may exhibit dramatically different patterns at different times, frequently switching back and forth among two or more relatively stable states. As the Earth spins, its rotation sets up waves in atmospheric circulations, much as water in a river rapid sets up standing waves. In such systems, it is natural that a wave crest or "high" in one region will be connected to wave troughs or "lows" in neighboring regions.

El Niño events are among the best known of these multiple-state patterns (Figure 2.14). During El Niño events, ocean circulation patterns change across the Pacific Ocean. Rain patterns shift and atmospheric circulation changes in response to alterations in ocean water temperatures. These effects are felt in the Pacific but are also reflected in other, far distant parts of the globe.



Normal conditions

El niño conditions

FIGURE 2.14 **El Niño.**

Periodically, the gross circulation of the southern Pacific Ocean changes, in a phenomenon known as El Niño. Under El Niño conditions, the thermocline becomes more shallow and upwelling is reduced along western South America. This results in pooling of warm water in the central Pacific and changes in precipitation and convection patterns. *Source: Lovejoy and Hannah (2005). Reproduced with permission from Yale University Press.*

Thus, El Niño years are associated with less upwelling of deep ocean water and enhanced rainfall in the Pacific but also with decreases in rainfall and drought in Africa. These long-distance effects are the result of global circulation patterns sitting next to, and driving, one another, almost like gears. What happens in one circulation cell is passed on to the next and may result in consequences in faraway places. Such long-distance, linked impacts are called

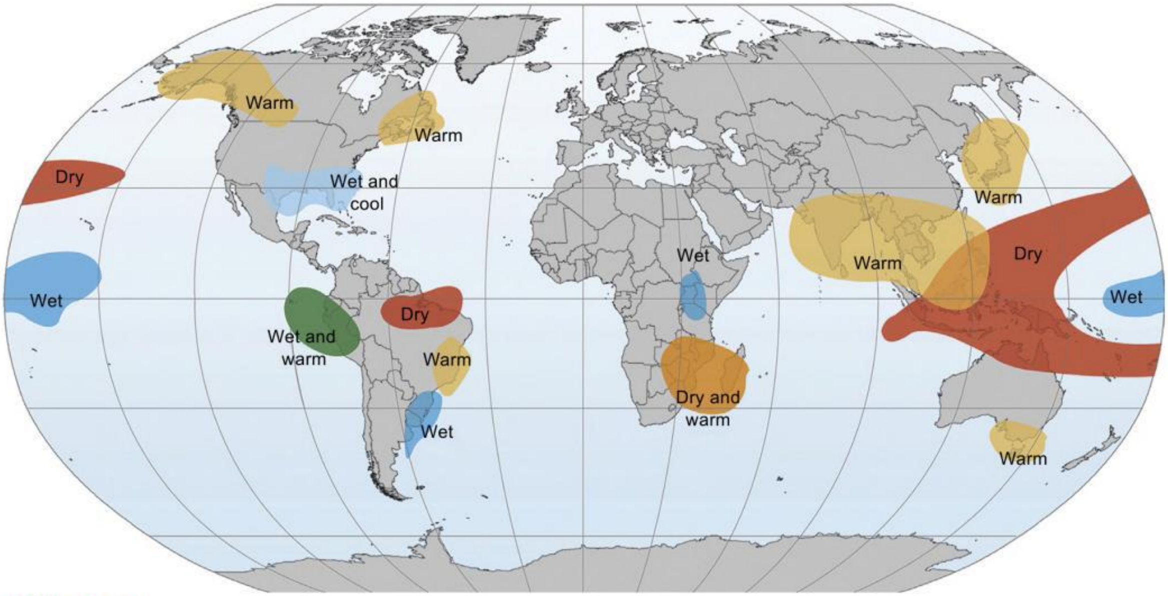


FIGURE 2.15 **El Niño teleconnections.**
Changes associated with an El Niño event include drying, warming, changes in precipitation, and cooling in different combinations in regions as widely separated as South Africa and Eastern Asia. *Source: Reproduced with permission from Mark Bush. Ecology of a Changing Planet, 3rd edition: Benjamin Cummings.*

"teleconnections (Figure 2.15)." Teleconnections are not random; they tend to be linked to complementary "sister" states. They often involve coupled changes in ocean and atmospheric states. For instance, the complement to El Niño conditions are La Niña events, in which upwelling in the Pacific is enhanced and rainfall reduced. The oscillation between these two conditions is known as the El Niño/Southern Oscillation or ENSO.

Other large-scale modes of atmospheric variability include the North Atlantic Oscillation and the Pacific Decadal Oscillation. The Pacific Decadal Oscillation affects the North Pacific Ocean and switches states approximately every 10 years, as its name implies. The North Atlantic Oscillation is dominated by two modes, one in which arctic air pounds Europe and another in which European weather is considerably more pleasant. The thermohaline circulation is an excellent example of a teleconnection because what happens in the North Atlantic may affect climate across the entire planet.

HUMAN-DRIVEN CHANGE: RISING CO_2

The rise of CO_2 due to fossil fuel burning and deforestation has been traced in a simple study on the Mauna Loa volcano in Hawaii. Air intakes atop the

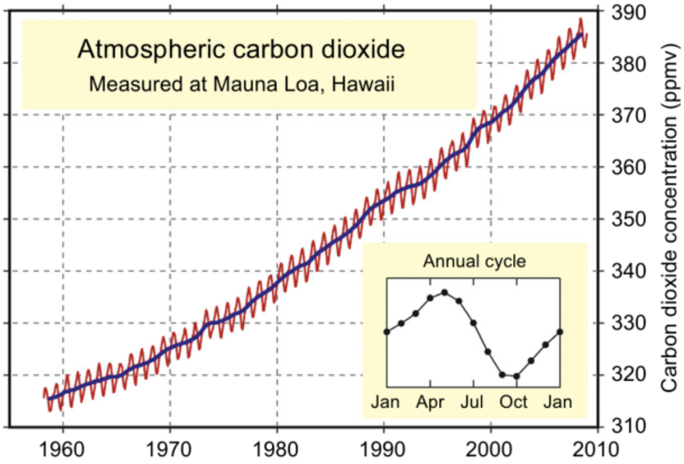


FIGURE 2.16 **Mauna Loa CO_2 record.**

The CO_2 record from Mauna Loa clearly shows strongly rising atmospheric CO_2 concentrations since approximately 1960. Superimposed on a multiyear increase is a much smaller "sawtooth" annual cycle, which results from the release and uptake of CO_2 from vegetation. *Source: From Climate Change (2007): The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.*

mountain capture samples that are then analyzed for CO_2 content. Mauna Loa was chosen because its island location and high elevation place it far away from short-term contamination from any city air pollution. The record of CO_2 at Mauna Loa is therefore pure: it shows what is happening in the atmosphere very plainly—and plainly CO_2 is rising dramatically (Figure 2.16).

CHARLES DAVID KEELING

Rising atmospheric CO_2 was first measured by Charles David Keeling at the Mauna Loa observatory on the island of Hawaii. Keeling worked at the Scripps Institute of Oceanography in San Diego and, along with Roger Revelle, the director of the institute, concluded that direct measurement of changing CO_2 was needed. In the late 1950s, Keeling settled on the remote slopes of Mauna Loa to escape local variation in CO_2 caused by urban emissions or vegetation. The program begun by Keeling continues today and has provided incontrovertible evidence of the effect of human pollution on the atmosphere.

The Mauna Loa record is so sensitive that it clearly shows the pulse of the seasons. Each spring, plants come to life, sucking CO_2 from the atmosphere. Then each fall, leaves fall and decompose, releasing CO_2 to the atmosphere as they decay. This cycle is balanced across the equator. As Northern Hemisphere plants die and release CO_2 in the fall, plants in the Southern Hemisphere are taking up CO_2 with the flush of new spring growth. However, landmasses in the north

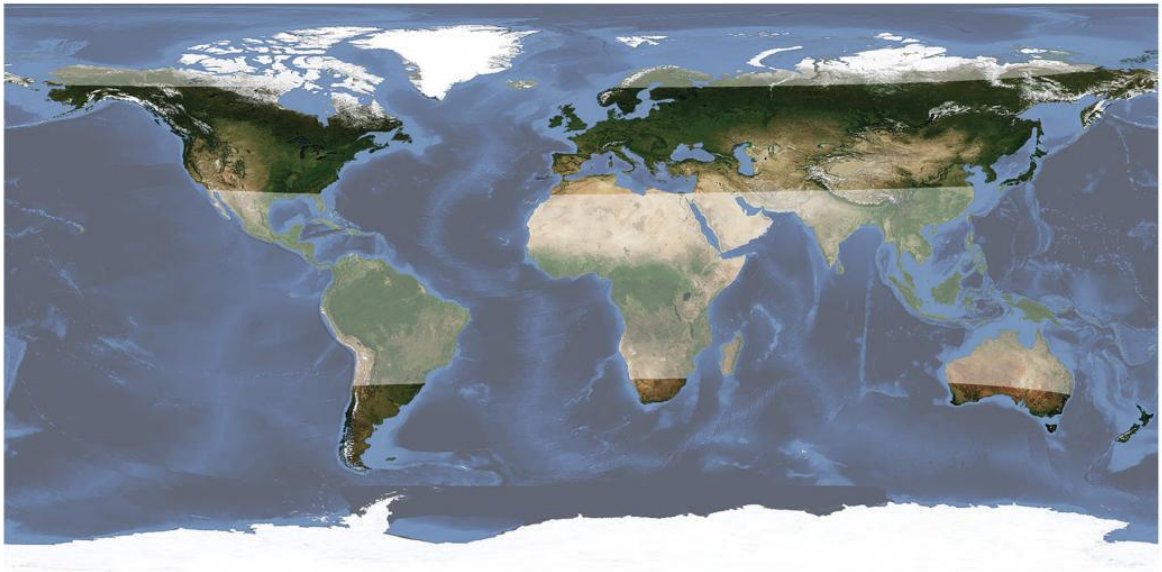


FIGURE 2.17 **Northern and Southern Hemisphere landmasses.**
Large amounts of land surface in the high latitudes of the Northern Hemisphere result in a large fall flush of CO_2 into the atmosphere and a large, measurable uptake of CO_2 from the atmosphere in the spring. The Northern Hemisphere effect dominates the same effect in the Southern Hemisphere because the Southern Hemisphere has little land at comparable latitudes. The dominance of landmasses in the Northern Hemisphere is also important in the formation of glacial periods. *Source: Courtesy of NASA.*

are far greater than those in the south (Figure 2.17), so Southern Hemisphere processes balance only a small part of the seasonal cycle in the north. A net global uptake of CO_2 occurs in the Northern Hemisphere in spring, with net CO_2 release in the Northern Hemisphere fall. This seasonal seesaw is reflected in the Mauna Loa record. The short-term drop in annual CO_2 during the northern spring is reflected in an annual blip of dropping CO_2 in the Mauna Loa record. A steep blip of increased CO_2 accompanies the northern fall each year in the Mauna Loa measurements.

CO_2 concentrations in the Earth's atmosphere are clearly and steadily rising. Each year, observers at Mauna Loa note slightly higher levels in both the spring highs and the fall lows—the annual seesaw in atmospheric CO_2 is slowly ratcheting up. This rise has been noted each year since about 1940, exactly as expected given the large amounts of oil, gas, and coal that are burned for fuel each year.

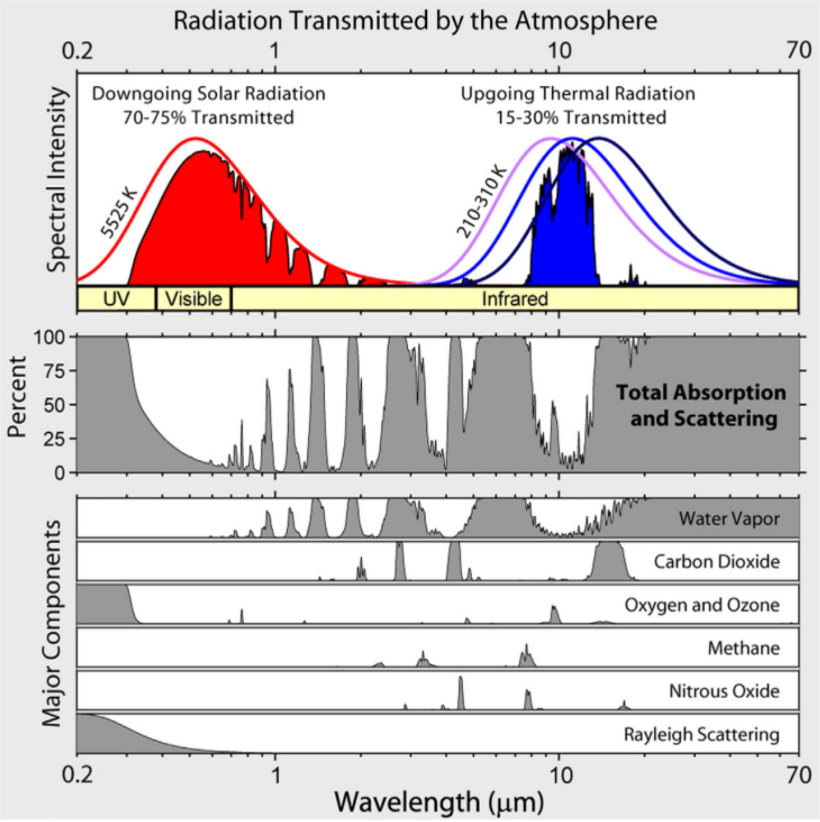
Fossil fuel use worldwide more than quadrupled in the period of the Mauna Loa record—from just over 2 Pg (as carbon) in 1960 to more than 8 Pg annually (a petagram (Pg) is 10^{15} g, or 1000 million metric tons) today. Clearing of forests and other land use changes contribute approximately one-fourth of total emissions of CO_2, for a global total of more than 8000 million metric tons a year.

ISN'T WATER A GREENHOUSE GAS?

Water is a greenhouse gas, one that absorbs in the same part of the spectrum as CO2 (see figure). Since water is much more abundant in the atmosphere than CO2, doesn't this mean that adding CO2 would have little effect on warming? Early scientists understood these gas absorption properties and as a result underestimated the greenhouse effect for nearly half a century.

What the scientists of the early 1900s didn't realize was that the Earth loses heat not at the surface where water vapor is abundant, but at the top of the atmosphere, where water vapor is essentially absent. At the top of the atmosphere, the absorbtion of CO_2 is dominant, and it doesn't saturate much at levels (4 times to 10 times preindustrial concentration) likely to be produced by human pollution.

So water is a greenhouse gas, but not where it matters – in the upper atmosphere. In the upper atmosphere where the Earth loses heat to space, the effect of CO_2 dominates. This is why the Earth is warming in response to human pollution.



Incoming radiation from the sun (red curve) and outgoing radiation from the surface of the Earth (blue curve) are both attenuated by absorption of photons by gases in the Earth's atmosphere. The resulting actual incoming (solid red) and outgoing (solid blue) radiation are the result of subtraction of the effects of various gases (labeled) and particles (Rayleigh scattering) in the atmosphere (gas absorption properties are shown in gray) from the theoretical total. *Figure courtesy of Global Warming Art, reproduced with permission.*

However, CO_2 is not the only greenhouse gas. Methane, water vapor, and other gases have warming effects (Figure 2.18), some of them much more pronounced than that of CO_2 (Table 2.1). Methane is particularly important because although it is a minor constituent of the atmosphere (its concentrations are measured in parts per billion), it has a strong warming effect—it is a potent greenhouse gas. Human activities produce methane, although in much

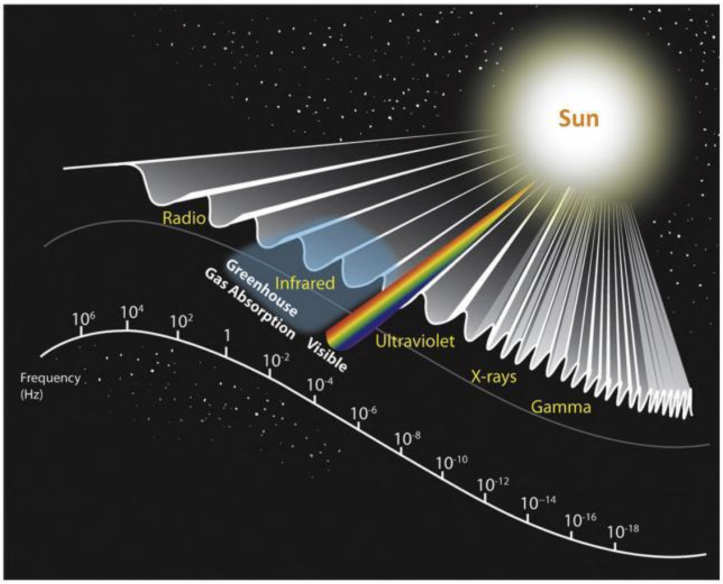


FIGURE 2.18 Electromagnetic absorption of greenhouse gases.
Electromagnetic radiation from the sun reaches the Earth as visible light, ultraviolet, or infrared radiation. This radiation strikes the Earth and is reradiated as longer wavelength radiation. Greenhouse gases such as CO_2 and methane absorb radiation in the portion of the spectrum that is just longer in wavelength than visible light. They then reradiate this energy, warming the atmosphere. *Source: University of California.*

Table 2.1 Greenhouse Gases, Potency, and Concentration

Gas	Global Warming Factor	Concentration in Atmosphere (ppb)
Carbon dioxide (CO_2)	1	379,000
Methane (CH_4)	21	1760
Nitrous oxide (N_2O)	310	320
Chlorofluorocarbons (CFCs)	5000–14,000	<1

ppb, parts per billion.
Source: IPCC.

smaller quantities than CO_2. Many types of farming result in methane emissions, with releases from decaying vegetation in flooded rice fields being the greatest source. Methane concentration in the atmosphere has increased from 700 ppb in preindustrial times to more than 1700 ppb today. Human activities do not strongly affect atmospheric water vapor concentrations directly, but water vapor concentrations are affected indirectly by temperature. Finally, some gases that are found in small amounts in the atmosphere and in human emissions are very strong greenhouse gases and may play a significant role in affecting global climate.

Because CO_2 in the atmosphere is currently increasing, we expect the climate to warm. This effect has been measured—global mean temperature is rising (Figure 2.19). Global mean temperature increased nearly 1 °C in the 100 years ending in 2005 (0.74 ± 0.18 °C (1.33 ± 0.32 °F)). The oceans generally warmed less than land so that most terrestrial regions, particularly continental interiors, have warmed in excess of the global mean (Figure 2.20). Some regions have cooled, whereas most have warmed. Cooling and warming trends are sometimes found in close proximity. Areas of Antarctica, for instance, have warmed as much as 2.5 °C, whereas other areas of the continent have cooled slightly.

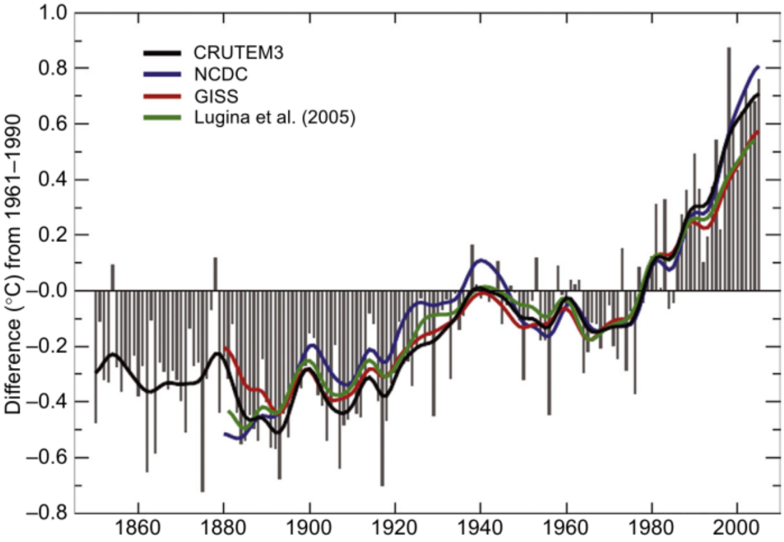


FIGURE 2.19 **Historic rise in global mean temperature.**

Units are deviation in degrees Celsius from the reference period 1961–1990. Colored lines represent temperature reconstructions using different methods. Bars indicate values from the instrumental record. *Source: From Climate Change (2007): The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.*

CLIMATE CHANGE OR GLOBAL WARMING?

Early descriptions of climate change often used the term "global warming." This phrase is less used today because scientists have documented so many manifestations of the effects of greenhouse gases in the atmosphere—including increases and decreases in precipitation, warming, and even short-term cooling—that the broader term "climate change" is preferred.

Global and continental temperature change

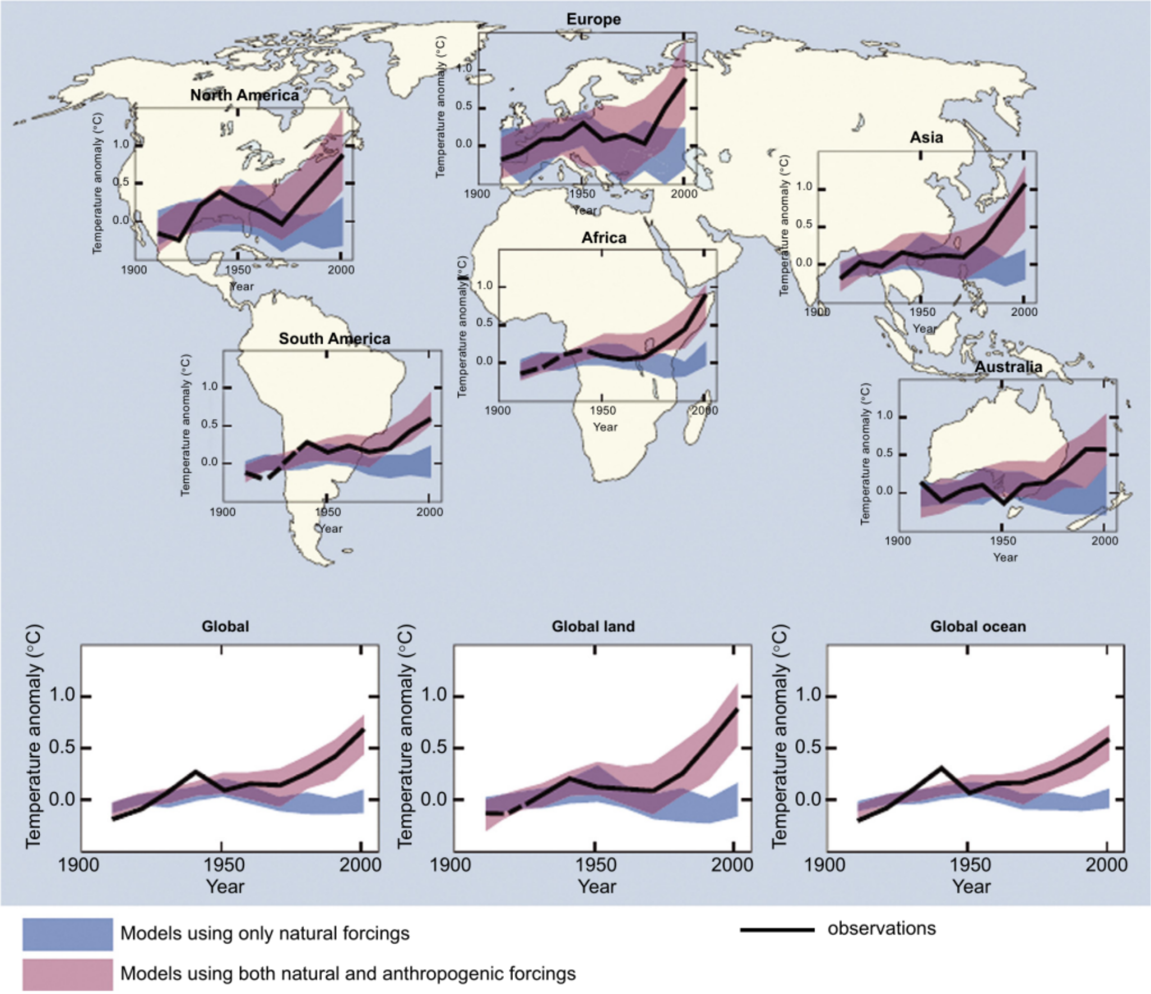


FIGURE 2.20 **Rise in mean temperature by continent matches human-driven climate change.**
Bold lines indicate historical record. Pink shading indicates the range of values from GCM simulations using both human and natural forcings on climate. Blue shading indicates range of values from GCMs forced with only natural (no human greenhouse gases) forcings. *Source: From Climate Change (2007): The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.*

RAPID CLIMATE CHANGE

Rapid climate changes have been very common in the transition to current warm conditions and for the past 2 million years. In fact, rapid climate shifts appear as far back as we have good methods for detecting them. There may be multiple causes for rapid change, but several mechanisms are emerging as especially important.

Shutdown of the thermohaline circulation (Figure 2.21) is one factor that clearly drives rapid climate change. Meltwater from land ice in Greenland and North America enters the North Atlantic during warming (Figure 2.22), causing the waters of the Gulf Stream to become less salty. This less saline water is less dense and thus cannot sink and complete the return trip to the equator. The thermohaline circulation shuts down, stopping transport of heat from the equator. The net result of the shutdown is colder conditions throughout the North Atlantic, especially in Europe.

THE POWER OF THE GULF STREAM

The Gulf Stream is a mass of warm water transported from the tropical Atlantic northward by the thermohaline circulation. The arrival of this warm water affects the climate of the North Atlantic, making northern Europe significantly warmer than it would be without the Gulf Stream influence. Without the thermohaline circulation, northern Europe would be plunged into a cold spell—an example of how climate change might even result in local cooling.

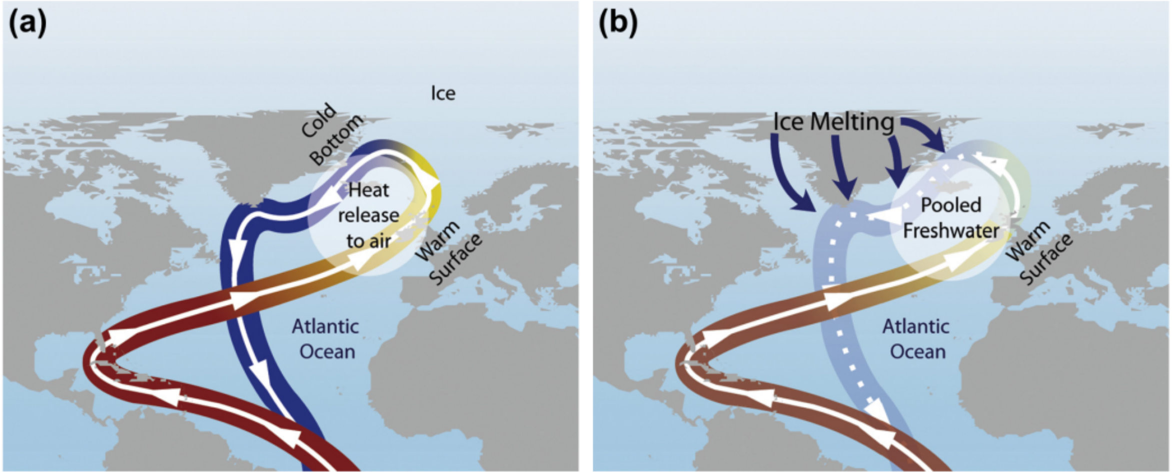


FIGURE 2.21 **Shutdown of thermohaline circulation.**
Thermohaline circulation is driven by dense water cooling and sinking (a). When polar ice melts (b), freshwater pulses in the North Atlantic can reduce contact of the Gulf Stream with ice and reduce its salinity. This leads to warmer, less saline water that is less likely to sink. If the freshwater pulse is strong enough, it can shut down thermohaline circulation.

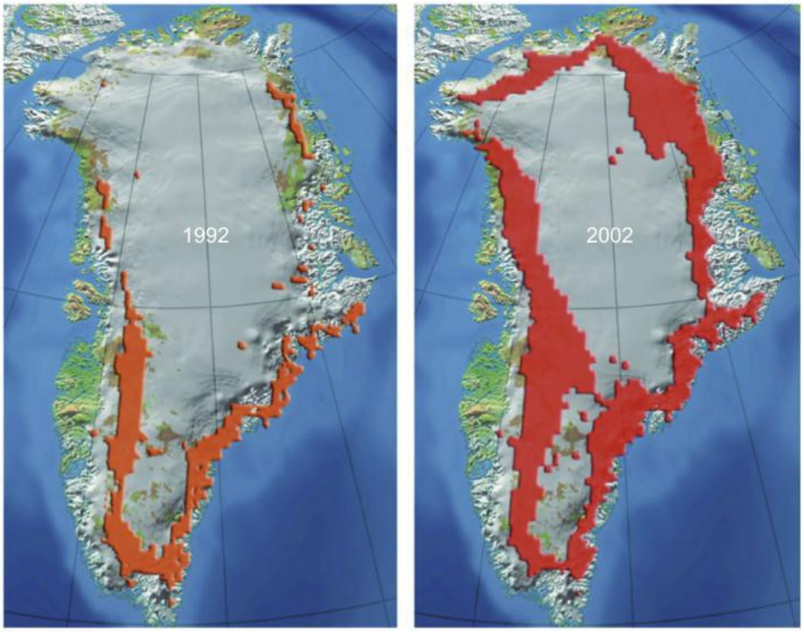


FIGURE 2.22 **Recent greenland ice melting.**
Red indicates areas of ice melt. Melt zones increased with warming in the latter half of the twentieth century. Greenland melt increases sea level rise, in contrast to the melting of sea ice (e.g., in Antarctica), which does not increase sea level because the ice is already displacing seawater. Continued acceleration of melting could result in shutdown of thermohaline circulation. *Source: Arctic Climate Impact Assessment.*

An example of thermohaline shutdown took place during the transition out of the last ice age. As conditions warmed, continental ice melted and meltwater entered the North Atlantic. The thermohaline circulation shut down, plunging Europe into a sudden cold snap lasting approximately 1000 years (Figure 2.23). The existence of this cold snap was first recognized in the remains of fossil plants. An arctic plant typical of ice age Europe, the mountain reinrose, was found in a narrow band of deposits dating to approximately 11,000 years ago. Scientists recognized that this indicated a brief cold snap in Europe. They named the cold snap for the plant. The Latin name for mountain reinrose is *Dryas octopetala*, and the name of the cold snap became the "Younger Dryas."

The Younger Dryas holds important lessons for the future because it was caused by warming that led to ice melt and thermohaline shutdown. An important question about future climate change due to greenhouse gas emissions is whether warming could again shut down thermohaline circulation.

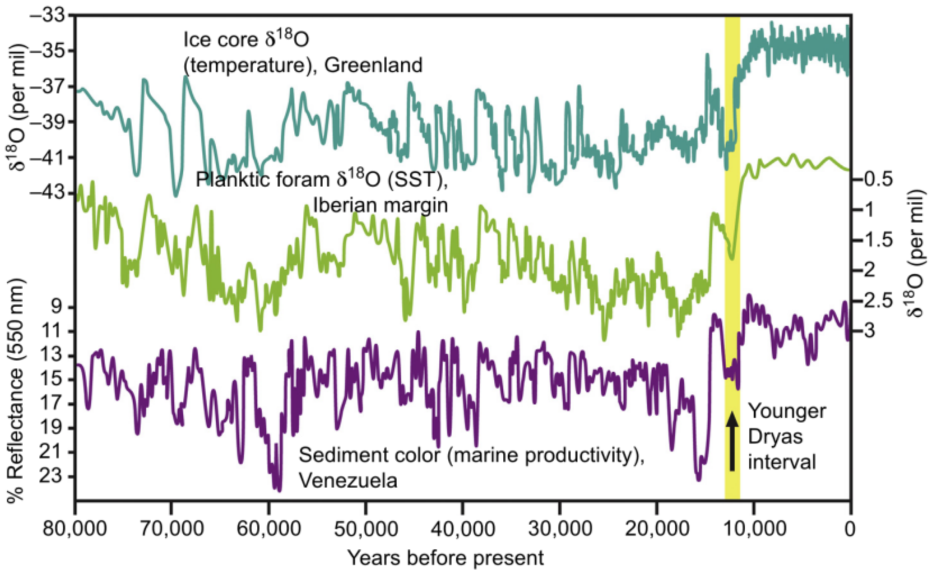


FIGURE 2.23 **The Younger Dryas in context.**
Temperature variation from three proxies shows very frequent, short climate flickers. All three proxies are in agreement on the frequency and relative timing of these flickers, indicating that they are global phenomena. The Younger Dryas event was a long-lasting climate flicker spanning about 1000 years that was particularly pronounced in Europe because it resulted from a shutdown of the Gulf Stream portion of thermohaline circulation. Note the relative stability of the warm climate of the past 10,000 years after the Younger Dryas. Human civilization has evolved in a period of atypical climatic stability. *Source: Reproduced with permission from Yale University Press.*

SPOTLIGHT: THE SEESAW EFFECT

Climate change does not unfold evenly on the two sides of the equator. Often, effects in one hemisphere are accompanied by changes opposite in sign in the other hemisphere or show up later in the other hemisphere. Alterations in northern sea ice extent are often an initiating event in these interhemispheric teleconnections, so that effects may be seen first in the Northern Hemisphere and then seen later or reversed in the Southern Hemisphere. This has been termed the "seesaw" effect.

Researchers see the seesaw effect in ice core proxies for temperature change. The "wiggles" of temperature change are indicated by oxygen isotope proxies in these cores. The wiggles in Antarctic ice cores do not match those in Greenland ice cores because of the seesaw effect.

Large, rapid changes in temperature are seen in the Greenland ice core record. Are these changes global? The answer seems to be no. Shackleton (2001) reviews research in this field and sees a seesaw of delayed change in the Southern Hemisphere rather than a global synchronous response. Rapid change in the Antarctic ice core seems to be offset from rapid changes in the Greenland ice core by thousands of years. Deep water temperatures in the Atlantic seem to follow the Antarctic pattern, whereas surface water temperatures follow the Greenland pattern.

The cause of the seesaw is most likely decoupling of climate connectivity across the equator. Circulation features such as Hadley cells originate at the equator, so there may be a delay in transmitting large changes across this boundary. Alternatively, the circumpolar current in the Antarctic could be a barrier to change, and the Antarctic climate may be out of synch with the rest of the planet. It has even been suggested that large abrupt change may originate in the tropics. Whatever the cause, Greenland and Antarctic ice core records clearly seesaw.

Source: Shackleton, N., 2001. Paleoclimate. Climate change across the hemispheres. Science 291, 58–59.

Other causes of rapid climate change may be associated with sudden releases of greenhouse gases such as CO_2 or methane. In the past, such releases may have occurred naturally from massive seabed deposits of methane hydrates, emissions from volcanic eruptions, or decay of vegetation associated with asteroid impacts. In the future, massive human emissions of greenhouse gases may have similar effects.

These emissions have massive effects on the global carbon cycle and are driving major changes in climate. Carbon cycle changes are important because they affect the balance that determines concentrations of CO_2 in the atmosphere and, hence, climate change.

***SPOTLIGHT*: HOTHOUSE OR ICE AGE?**

Previous interglacial periods have typically lasted approximately 10,000 years. The current warm climate has lasted more than 10,000 years: Are we headed for another ice age?

The answer seems to be "no." The orbital forcings that create interglacial periods are in an unusual configuration that has not been seen for approximately 400,000 years. The last time the Earth's orbit was in a similar configuration, there was an unusually long interglacial period. That interglacial period is known as Marine Isotopic Stage 11 (MIS 11).

One clue about MIS 11 comes from Antarctic ice cores. Raynaud et al. (2005) unraveled folds in the Vostoc Antarctic ice core to examine MIS 11 more closely. Once they had corrected for a fold in the ice, it became clear that MIS 11 was unusually long and that greenhouse gas concentrations were high. Another piece of evidence came from a simple three-state model of ice ages. This modeling showed that the current combination of orbital tilt and eccentricity is likely to lead to an interglacial period of 20,000–30,000 years.

Humans are now pumping greenhouse gases into the atmosphere that will accentuate an already warm climate. If orbital conditions were typical, we might expect that warming to delay the advent of the next ice age. However, with the next ice age tens of thousands of years away, human warming is likely to take climate to temperatures not seen in millions of years.

Source: Raynaud, D., Barnola, J.M., Souchez, R., Lorrain, R., Petit, J.R., Duval, P., et al., 2005. Palaeoclimatology: the record for marine isotopic stage 11. Nature 436, 39–40.

THE VELOCITY OF CLIMATE CHANGE

Another way to look at the rapidity of climate change is the velocity of temperature change. The velocity of climate change is proportional to the distance that has to be traveled over the surface of the Earth to maintain a certain temperature as climate changes (Figure 2.24). This speed varies depending on terrain. On a perfectly flat smooth Earth, maintaining a constant temperature requires shifting north or south with latitude, toward the cooler poles to offset warming. This latitudinal shift sets the velocity of climate change in areas with little topography. In mountainous areas, a similar temperature change can be achieved by shifting upslope, and these distances are much shorter. In the real world, with topography, flat areas have a high velocity of climate change and mountains have a low velocity of climate change.

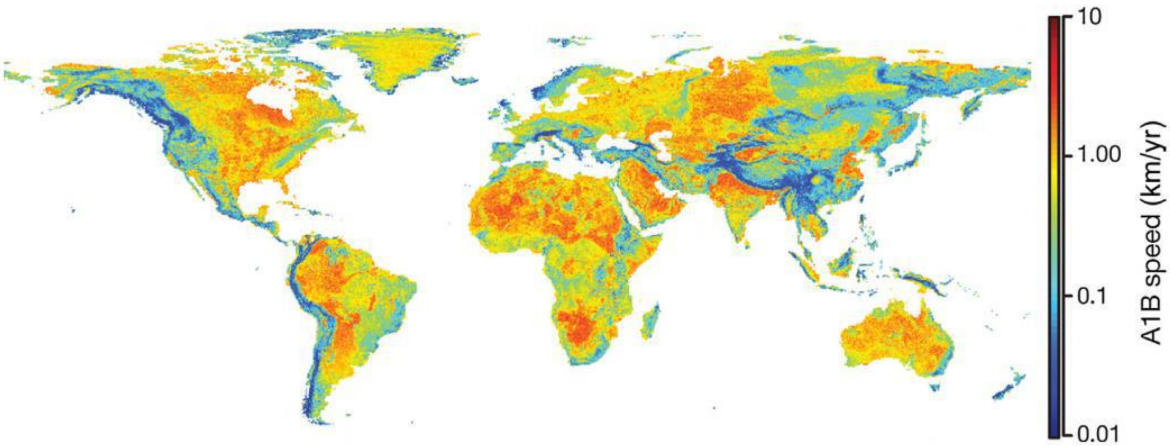


FIGURE 2.24 **Velocity of climate change.**
A global map of the velocity of temperature change shows the variation in speed of temperature change across the surface of the Earth. Velocity of climate change is the product of atmospheric temperature change and topography. Flat areas require latitudinal movement to track atmospheric temperature change and have a high velocity of climate change. Mountainous areas can track temperature change upslope across much shorter distances and so have a low velocity of climate change. *Source: Loarie et al (2009). Reprinted with permission from Nature.*

Velocity of climate change matters to living things, especially plants. Plants are mobile only when seed disperses, which makes keeping up with the velocity of climate change a problem. Plant dispersal may have trouble keeping pace with temperature shifts where the velocity of climate change is high. In the mountains, the velocity of climate change reduces the distances that plants have to cover to keep pace with climate change, but gravity may work against some dispersal mechanisms. Most obviously, gravity-dispersed seeds will move downhill, in the direction opposite of temperature shifts. Understanding the velocity of climate change and its interplay with species' dispersal is therefore important to understanding both past and future range shifts.

MODELING THE CLIMATE SYSTEM

Climate change models allow the simulation of the effects of the buildup of greenhouse gases centuries into the future, based on current understanding of atmospheric physics and chemistry. The typical horizontal resolution of a global climate model is 100–200 km. Combining global and regional models allows finer-scale examination of regional details of change to horizontal resolutions of 10–50 km. Most global models are run on supercomputers, whereas some regional models may be run on desktop computers (often taking six to eight months for a single realization).

STRUCTURE OF GENERAL CIRCULATION MODELS

General circulation models (GCMs) use a system of mathematical equations to simulate the movement of mass and energy from one part of the atmosphere to another. They divide the atmosphere and ocean into a series of three-dimensional cells, each of which transfers mass and energy to its neighbors based on the outcome of the equations within the cell. These are in principle the same type of model used to predict weather, but they are run on a broader (global) scale and for centuries rather than days.

Global climate models simulate climate changes across the entire planet. These models are often referred to as GCMs because they simulate general atmospheric circulation patterns. GCMs represent atmospheric and ocean circulation in a series of equations describing physical properties of gases and fluids. Each set of equations is solved for a volume of air or water, typically with dimensions of hundreds of kilometers. The atmosphere and oceans are represented by thousands of these cubes, distributed 10–20 layers thick across the face of the planet and down into the oceans. Energy and water vapor (or liquid) are passed between the cubes, allowing simulation of ocean currents and circulation in the atmosphere. This process is similar to that for models used to forecast weather, except it is applied over broader spatial scales to capture global effects and on longer timescales to capture climate instead of weather. Because of these broader spatial and temporal scales, the resolution of GCMs must be much coarser than that of weather models to stay within the computational limits of modern computers.

EVOLUTION OF GCMS

Models of global climate began as mathematical descriptions of atmospheric circulation. They were known as general circulation models or GCMs. As the models became more complex, layers of ocean were added. These models were known as coupled atmosphere–ocean GCMs (AOGCMs). Today, most GCMs are AOGCMs. More advanced models incorporate the effects of vegetation change on climate, effectively joining models of the biosphere to the ocean–atmosphere models. These most advanced models are known as earth system models.

Regional climate models (RCMs) are very similar in structure to GCMs, but they capture finer-scale resolution of change in a particular region (Figure 2.25). The equation-based processing, cubes, and layers of the GCM are all present in an RCM but at finer scale. The scale of an RCM is measured in tens of kilometers, as opposed to hundreds of kilometers for most GCMs. In exchange for higher resolution, RCMs must be run for regions, rather than for the whole planet, as their name implies. This trade-off of resolution for geographic scope is required by the limits of computational time required to run the model. Model runs of more than a week on a supercomputer are usually prohibitively expensive because the model must compete for other uses of the specialized computing facility, such as weather forecasting. Because the climate of one region is connected to the climate of neighboring regions, RCMs cannot be

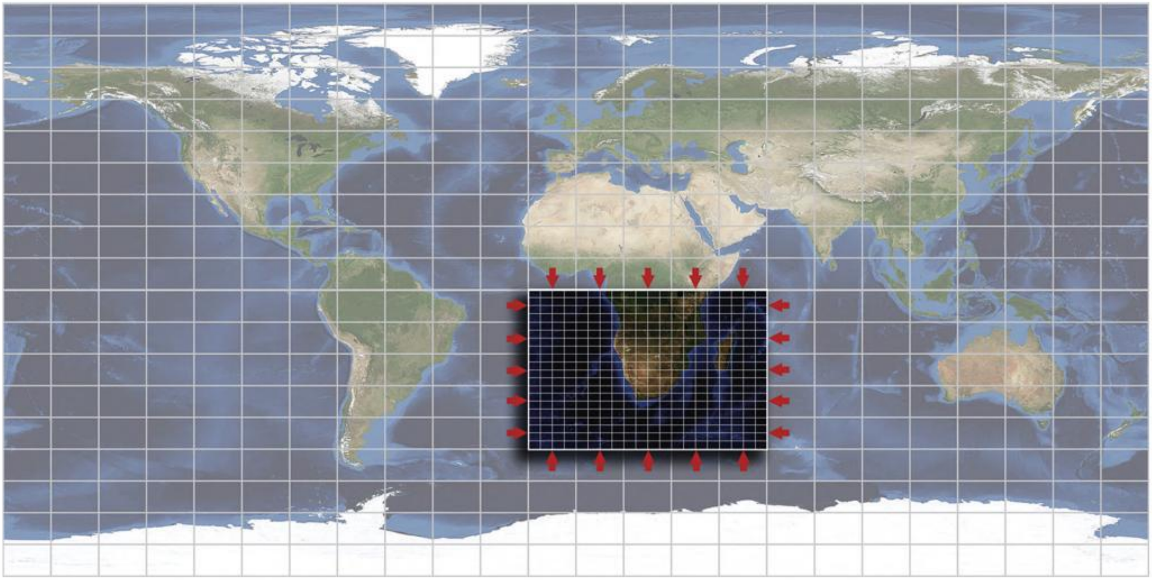


FIGURE 2.25 Regional climate model.
Regional climate models (RCMs) are run embedded in general circulation models (GCMs). They receive information at their boundary from the GCM. An RCM therefore cannot rectify errors in a GCM. It can, however, improve the simulation of regional change by resolving processes that cannot be captured at the resolution of a GCM. Here the domain of an RCM is illustrated embedded within the domain (global) of a GCM. Red arrows indicate transfer of information from the GCM to the RCM. *Source: Courtesy of NASA.*

run alone; they must be connected to other regions in some way. The most common way for an RCM to be connected to global climate is to embed an RCM into a GCM. The RCM then takes coarse-resolution GCM inputs at its edges and turns them into a finer-scale regional climate simulation.

The trade-off between spatial resolution (scale) and geographic scope (domain) of a model forces the use of adaptations of GCMs to address special problems. For instance, to study atmospheric phenomena in more detail, climate modelers will sometimes use a high-resolution atmospheric model but will couple it to a static ocean model to save computational demands.

NO MEAN TEMPERATURE

Global mean temperature is the political yardstick often used to measure climate change impacts and the success of international policy efforts. It is a simple and clear metric for these purposes, but it is the wrong metric for biological analyses. Biological impacts happen in specific places that all have their own unique climate characteristics important to species' survival—the global mean fuzzes all these meaningful regional variations into one number. For instance, the variation between islands, which are much cooler because their climates are dominated by cooler oceanic temperatures, and continental interiors, which are relatively much warmer, is completely obscured in global mean numbers (Figure 2.26). Global mean temperature is fine for international policy dialog, but biologists need to pay attention to regional on-the-ground variation.

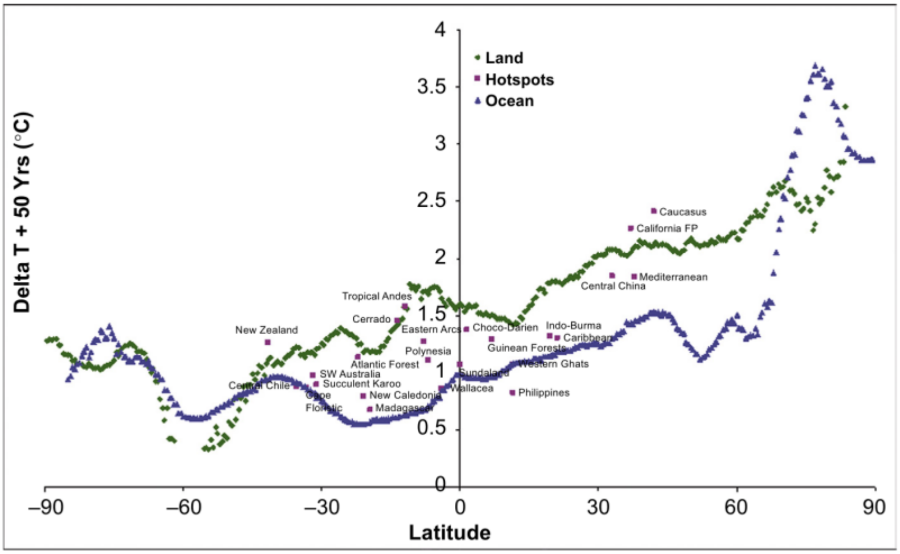


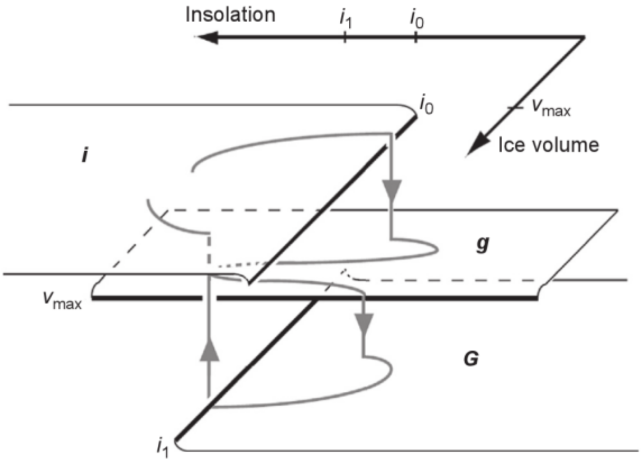
FIGURE 2.26 **Global biodiversity hot spots and future temperature change.**
Temperature versus latitude in a Hadley Center general circulation model (GCM) simulation for 2050 (A2 scenario). Blue circles indicate mean temperature change in the ocean at a latitude, green circles indicate mean temperature change over land for the latitude. Temperature change over oceans at midlatitudes is less than temperature change over land owing to the heating properties of water and continental interiors. Mean temperature change in the global biodiversity hot spots is indicated by red squares, for comparison. Note that island hot spots fall near the oceans line, while continental hotspots fall near the land line.
Source: Lovejoy and Hannah (2005). Reproduced with permission from Yale University Press.

GCMs are also used to establish the role of human emissions in climate change. For these assessments, GCM simulations are run for the recent past using only natural drivers of climate change and compared to observed warming trends (see Fig. 2.20). In general, GCMs are able to reproduce the full range of warming that has been observed since the last decades of the twentieth century only when human drivers of change ("human forcings") are included in the models. This is generally taken as strong evidence that human pollution is the cause of recently observed climate change.

Reconstructing past climates may be done with GCMs to either validate the models or investigate possible past conditions. GCMs may be tested by determining if they can reproduce past climates. Of course, past climate in these tests must be reconstructed from other sources, such as pollen records. Often, the past record is not robust enough to provide a very detailed test of GCMs, but GCMs can be tested to determine if they can reproduce the broad outlines of past climate, such as temperature changes over thousands of years. Because pollen and other records of past climate are fragmentary, GCMs can also be used to explore gaps in our understanding of past change. For example, GCMs have been used to try to explore the role of greenhouse gas forcing in past climates.

There are some types of past change, however, that GCMs do not represent well. Transitions between glacial and interglacial periods are not reproduced well by GCMs. This is probably because of positive feedbacks not captured well even by sophisticated current GCMs. Simpler models that simulate transitions between multiple states better reproduce glacial–interglacial transitions.

STATE MODELS FOR GLACIAL–INTERGLACIAL PERIODS



Schematic of simple three-state model of glaciation.
The diagram illustrates transitions between interglacial (i), mild glacial (g), and full glacial (G) climate regimes regulated by insolation and global ice volume. This model illustrates an i-G state transition when insolation drops below a critical threshold (io), with the depth and persistence of glacial states (g, G) determined by the existing ice volume as insolation changes. *Source: Palliard, 1998.*

Glacial-interglacial transitions are not well simulated in GCMs, but simpler "state" models reproduce some of the behavior of these transitions remarkably well. A state model represents glacial conditions as one state, with interglacial conditions as a second state, with transition coefficients between the two. These simple models are sometimes used to explore glacial–interglacial dynamics because GCMs, for all their complexity, cannot yet reliably simulate state-transition dynamics.

REGIONAL CLIMATE MODELS

GCMs provide some insight into climate changes on regional scales relevant to assessing impacts on biological systems, but the utility of GCMs in regional work is limited by their coarse scale. Most GCMs are run at scales of hundreds of kilometers, which means that a subcontinent may be represented by as few as five or six cells in the GCM. This means that many features that will be important in determining orographic rainfall and other important climate phenomena will not be resolved at the scale of the GCM.

For instance, in a GCM, all of the mountains of western North America will be represented as a single large "hump" that extends from the Sierra Nevadas of California to the Rocky Mountains (Figure 2.27).

To solve this resolution problem, RCMs are used. RCMs operate on the same principle as GCMs but with cells of considerably smaller dimensions—typically 10–80 km on a side. Because the dimension is squared to get the area of the cell, and cubed to get its volume, an RCM at 50 km has more than 100 times greater resolution than a GCM at 300 km.

The greater resolution of the RCM allows representation of mountains and other topographic features with greater fidelity. This in turn allows simulation of orographic rainfall, temperature variation with altitude, and other features lost in coarse-scale GCMs. The resolution of GCMs and RCMs is typically given as the

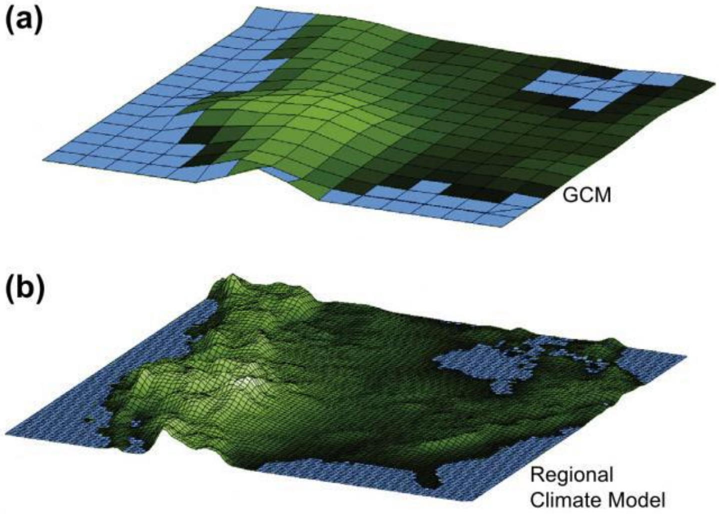


FIGURE 2.27 **Regional climate model (RCM) resolution.**
An RCM can resolve features such as mountain ranges that have important influences on climate. In this example from North America, all mountains from the Sierras of California to the Rocky Mountains are represented as a single hump at the horizontal resolution of a GCM, whereas they are better resolved at the resolution of the RCM. *Source: Lovejoy and Hannah (2005). Reproduced with permission from Yale University Press.*

length of one side of a grid cell, or horizontal resolution. The horizontal resolution of modern GCMs is typically 80–300 km, and that for RCMs is 10–80 km.

An RCM must be embedded in a GCM to function. At its edges, the RCM needs information about conditions in neighboring cells. For instance, an RCM cannot simulate orographic rainfall unless it knows the amount of moisture entering the region. These neighbor cell conditions, or "boundary conditions," are provided by the GCM in which the RCM is embedded (see Fig. 2.25).

The higher resolution of an RCM is appropriate for many regional impact assessment applications. At finer horizontal resolution, rainfall changes over many areas of a region may be resolved. Temperature changes, such as up-mountain slopes, can be resolved at scales relevant to cities, watersheds, and other planning units.

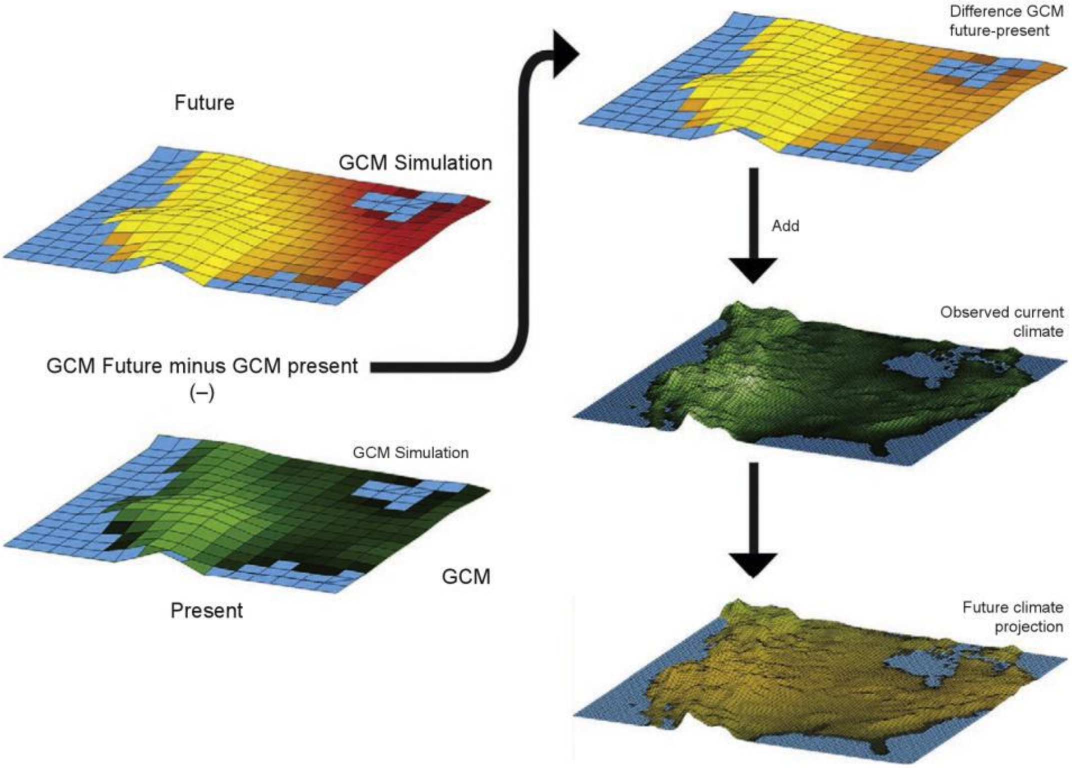
STATISTICAL DOWNSCALING

GCM projections are translated for regional impact assessment using either statistical or dynamic downscaling. Dynamic downscaling nests a fine-scale climate model (or RCM) within a GCM. Statistical downscaling uses observed relationships between large-scale climate phenomenon and local conditions to generate fine-grain projections from GCM output. For instance, rainfall at a site may be correlated with synoptic conditions such as regional atmospheric pressure fields. If such a relationship exists, it can be used to project future rainfall using pressure fields simulated by a GCM. Biologists doing regional impact assessment need to be aware of alternative downscaling methods because GCM simulations are too coarse to be useful in these applications.

For many biological applications, however, even 10–80 km is still very coarse. Movements of large animals in a landscape occur on scales of a few tens of kilometers. Movements of small animals may occur on scales of meters or kilometers. Plant dispersal events, particularly for structural species such as trees, may occur on scales as small as a few meters.

To address these relatively fine-scale phenomena in biological assessments, further reduction in scale may be achieved through smoothing and interpolation. In this process, present climate data are interpolated to a desired scale, such as 1 km. The difference between present and future GCM simulations is then added to the interpolated current climate data, yielding a future climate surface at the desired scale. The edges of GCM cells are smoothed to avoid "blocky" changes in the future surface. This process may be used to reduce either GCM or RCM (or statistically downscaled) data to fine scale. Much current biological impact assessment in species distribution and dispersal is now done with climate surfaces at a 1-km scale using this technique (available for download at sites such as Worldclim.org).

DOWNSCALING SIMPLIFIED



One approach to generating finer-scale regional climatologies from GCMs is simpler than either statistical downscaling or RCM approaches. The difference method subtracts the present value for a variable of interest, such as temperature, that a GCM projects from the future projected value. This difference is then added to current observed climate for that variable to obtain an estimate of possible future values. The difference method is used because GCMs do not faithfully reproduce present climate at fine scales, so comparing future GCM projections to observed climate may result in errors. The method takes the amount of change from the GCM but the spatial and temporal variability from observed (current) climate.

COMMONLY USED GCMs

Many GCMs exist, developed by universities, research centers, and national weather services. All are run on supercomputers or massively parallel computers. All use similar suites of physical equations but differ in the specifics of particular equations, complexity, and treatment of parameters.

SUPERCOMPUTERS AND MASSIVELY PARALLEL COMPUTERS

Source: Supercomputers. Courtesy of NOAA.

GCMs employ complex equations in a simulation of the entire globe, making them very computationally intensive. This means that an individual GCM simulation will take a long time to run on a conventional computer. To speed runs, supercomputers with large memory and processing capability are used. These are often the very same supercomputers that are used to run weather forecasts, although climate change research centers, such as Britain's Hadley Centre, have their own dedicated supercomputers. A less expensive alternative is to join many smaller workstations in parallel. Such systems are called massively parallel computing systems and have become an option for smaller labs and even some major international centers.

Most assessments of climate change use simulations from more than one GCM because no model simulates the future perfectly. Using more than one GCM therefore helps researchers explore the uncertainty in possible future climates. It is therefore important that several credible GCMs are available to choose from.

Among the best known and most widely used GCMs is probably that of the Hadley Centre in Britain. The Hadley Centre is a branch of the weather service (Meteorological Office or Met Office) in the United Kingdom. The Hadley Climate Model or HadCM is a relatively sophisticated model that includes active interaction between climate and land cover.

Other GCMs frequently used in impact assessments include the Community Climate Model produced by a consortium of universities (the climate research "community") led by the National Center for Atmospheric Research in Boulder, Colorado; the Canadian Climate Model produced by a research group at the University of Victoria using the supercomputer of the Canadian Weather Service; the GFDL model created by NASA's General Fluid Dynamics Laboratory; and the CSIRO GCM run by the Commonwealth Scientific and Industrial Research Organization in Australia. For most assessments, several of these models are used—often those that do particularly well at simulating current climate for the region of interest, though increasingly, ensembles of large numbers of GCMs (30+) are becoming best practice in impact assessments.

Assessments must also make assumptions about the magnitude of future greenhouse gas emissions. Humans are using increasingly more fossil fuel each year, resulting in increasing emissions of CO_2 and rising atmospheric CO_2 levels. How fast those emissions continue to grow will determine how fast and how much climate will change. No one knows with certainty how future energy use will unfold, so assumptions must be made in every GCM about how much CO_2 is released into the atmosphere over the time period being modeled.

EMISSIONS PATHWAYS

The Intergovernmental Panel on Climate Change (IPCC) has prepared a series of standard greenhouse gas concentrations for use in GCM simulations. These are known as Representative Concentration Pathways (RCP). Each RCP represents one possible trajectory for future greenhouse gas concentrations. Previous IPCC assessments have used emissions scenarios, with identifying codes such as A1 and B2. These are now outdated, though sometimes still an important source of information. The RCP series was constructed from a range of possible emissions curves, rather than from global storylines. The RCPs allow assessment of the implications of a range of possible pathways, including 'overshoot' scenarios in which global greenhouse gas concentrations exceed a policy target (e.g., 2° C global mean temperature change) and then return to the target level.

IPCC

The Intergovernmental Panel on Climate Change was formed in 1988 by the World Meteorological Organization to help promote a scientific and political consensus about the occurrence and impact of climate change. Leading climatologists and impact researchers conduct reviews of climate change research for the IPCC, which are then submitted to a vetting process open to all 192 United Nations member governments. Previous IPCC reports have been issued in 1990, 1995, 2001, and 2007. The current IPCC report is the fifth. The IPCC shared the Nobel Peace Prize with Al Gore in 2007.

Each RCP is identified by a number corresponding to the watts per square meter (W/m^2) forcing associated with the greenhouse gas concentrations in 2100 (Figure 2.28). For example, RCP6.0 is a pathway with a forcing of 6.0 W/m^2 in 2100. RCP2.6 is an 'overshoot' pathway, in which atmospheric CO_2 rises and then falls. RCP8.5 is most similar to current emissions trends.

GCM OUTPUTS

The equations of a GCM produce "weather"—daily rainfall, temperature, and winds values. However, most of these outputs are not saved in a GCM run. It is simply not practical to save such large amounts of data. Instead, summary statistics are saved, such as mean monthly rainfall and mean temperature. This allows a profile of the run to be saved without taking up huge amounts of storage space with unneeded data. The GCM output is often further simplified to produce a trace of global mean temperature increase (Figure 2.29).

However, GCM runs do not always save the data most relevant to biological analysis. Organisms may respond to extreme events, such as drought or severe

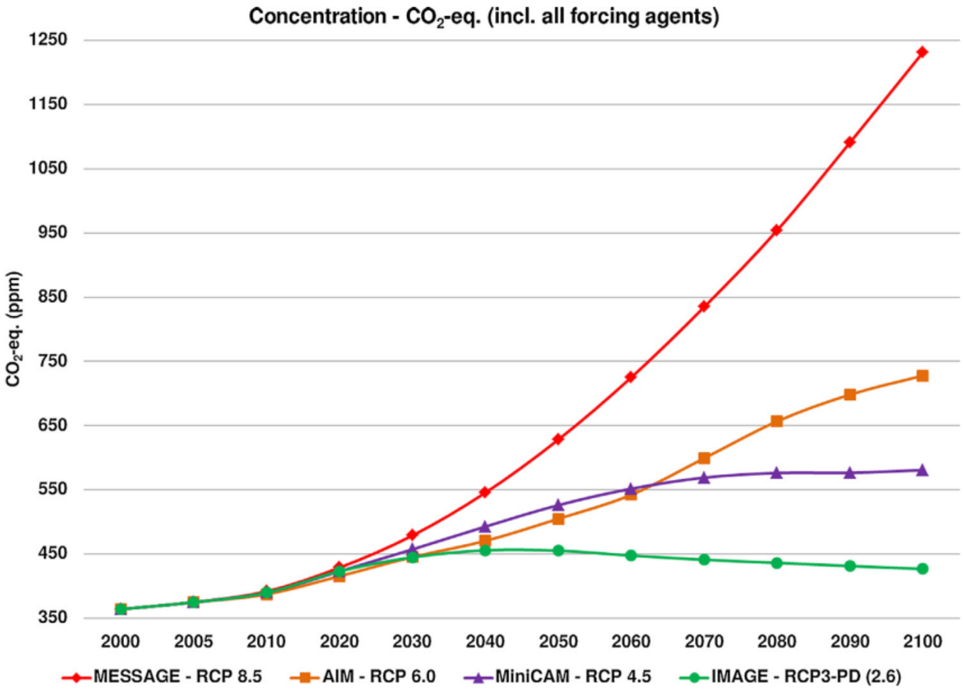


FIGURE 2.28 **Representative concentration pathways.**
The Intergovernmental Panel on Climate Change (IPCC) defines possible future buildup of greenhouse gases in the atmosphere as representative concentration pathways (RCP). RCPs represent atmospheric greenhouse gas concentrations resulting from possible differences in future emissions. Higher concentrations will result from higher emissions and lack of action to curtail emissions, whereas lower concentrations may result from lower economic growth or active efforts to reduce greenhouse gas emissions. RCP units are watts per square meter, corresponding to the radiative forcing of various concentrations in 2100. This figure shows the CO_2 equivalent of each RCP, the atmospheric concentration of CO_2 required to have a forcing equivalent to all greenhouse gases in the RCP (CO_2, methane, etc.). *Source: IPCC 2014.*

storms, that are not captured in mean monthly statistics. Biological studies may use typically archived statistics or work with climatologists to have more biologically meaningful outputs saved or extracted from GCM runs.

ASSESSMENT USING MULTIPLE GCMS

Assessments of climate change impacts may focus on individual disciplines, such as biology or agriculture, or be integrated multidisciplinary assessments. In either case, the use of multiple GCMs is recommended. Assessing possible outcomes against a variety of GCM projections can help capture uncertainty about possible futures. For instance, for many regions, projected change in rainfall varies from an increase in some GCMs to a decrease in others. Using several projections can help bracket these possible outcomes. In some circumstances, taking ensemble combinations of GCM projections can be more accurate than using them separately to bracket possibilities. Whatever approach is used, the use of several GCMs improves the credibility of impact analysis, whereas the use of too many GCMs results in a welter of findings that are difficult to sift through.

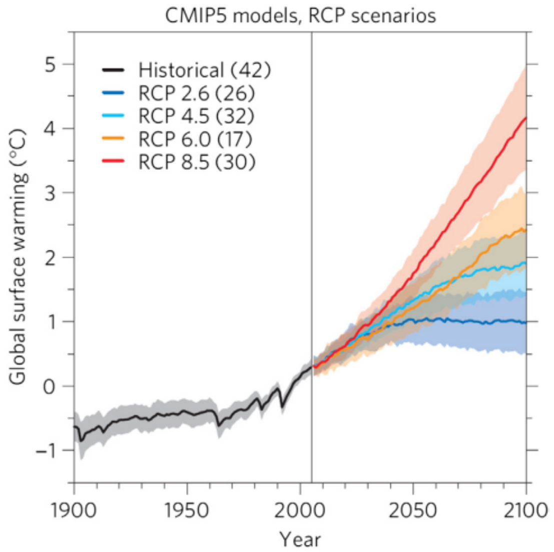


FIGURE 2.29 **Global mean temperature estimated from general circulation models (GCMs).** Using representative concentration pathways (RCP) scenarios, GCMs simulate global climate change. One summary statistic from these simulations is global mean temperature, shown here as it varies with RCP (heavy colored lines) and GCM (shading around colored lines). *Source: From Knutti and Sedlacek (2012). Reproduced with permission from Nature.*

BIOLOGICAL ASSESSMENTS WITH DOWNSCALED DATA

Assessments use GCMs to provide climate simulations against which biological changes can be judged. Such assessments can use either statistical or mechanistic models. Mechanistic models use equations describing biological processes such as photosynthesis to infer change in vegetation type or disturbance. Statistical models use statistical relationships or equations simulating biological processes such as photosynthesis to drive a specific quantitative result with GCM input. For instance, the vegetation type can be simulated by a dynamic global vegetation model, or habitat suitability for a species can be simulated with a species distribution model.

FURTHER READING

Intergovernmental Panel on Climate Change, 2013. Climate Change 2013: The Scientific Basis; Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Intergovernmental Panel on Climate Change, 2014. Climate Change 2014: Impacts, Adaptation and Vulnerability; Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Intergovernmental Panel on Climate Change, 2014. Climate Change 2014: Mitigation of Climate Change; Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

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2

SECTION

The Impacts of Human Induced Climate Change

CHAPTER 3

Species Range Shifts

Climate determines where plants and animals can live. Plants and animals all have an "address"—the combination of conditions in which they can survive and reproduce. This address is called their *niche*: by definition, organisms cannot survive outside of their niche.

Climate plays a major role in defining the niche of all species. Temperatures too hot or too cold, too much moisture or too little, all determine where plants can grow and where animals can survive. If you have tried to grow a palm tree in New York City or raise pears in Phoenix, you know that plants cannot flourish where the climate is wrong for them. Palm trees are killed by frequent New York frosts, and pears do not get enough chilling to set fruit in Phoenix. The niche space in which species can survive is determined in large part by suitable climatic conditions.

Species' ranges shift over time to track suitable climate. When climate changes in a location, some species may find themselves in suddenly hostile conditions. Others will find that previously unsuitable climates have changed in their favor. Individuals in unsuitable conditions will die or fail to reproduce, gradually disappearing from the location, whereas individuals near newly suitable habitat will gradually occupy areas in which they have not occurred previously.

GRINNELLIAN AND HUTCHINSONIAN NICHES

Joseph Grinnell first used the term niche in 1917. Charles Elton (1927) described species niche as something akin to an occupation: it was what the species did to survive, or its role in a biological community. Later, G. Evelyn Hutchinson expanded the concept to include the full range of environmental conditions that determine a species' fitness or survival. The Hutchinsonian niche is more analogous to a species' address. Climate change biologists are interested in the range of climatic conditions that determine a species' distribution and therefore more frequently employ the Hutchinsonian concept of niche.

When climate changes too rapidly, extinctions may occur. However, extinction is not always or even most often the end result of climate change. More often, species are able to track suitable climatic conditions, occupying new areas and leaving unsuitable locations as climate changes, a process sometimes termed "niche tracking."

Climate Change Biology. http://dx.doi.org/10.1016/B978-0-12-420218-4.00003-2

SPECIES RANGES

A species' range is the area in which it is found, including both its extent (extent of occurrence) and the locations within that extent that are actually occupied by the species (area of occupancy). Range is determined by the spatial distribution of individual populations. Abundance, which is often governed to some degree by climate, determines whether populations endure. When populations are lost on the range periphery, or when new populations appear that expand the range, a range shift occurs.

Range shifts can be driven by long-term changes in mean climate state, by short-term climatic extremes such as freezing, or by interactions with other species being driven by climate change. Many examples of each of these types of shifts have already been observed owing to climate change. Managing these movements is one of the great challenges for conservation in the twenty-first century.

This chapter focuses on range shifts of plants and animals in terrestrial, marine, and freshwater systems. These are among the most dramatic and best understood of the mounting biological impacts of human-driven climate change. The evidence is accumulating quickly and is far from complete—there are certainly major changes yet to be documented. However, the overall body of evidence clearly shows that range shifts are occurring in many species in response to global warming and changes in other climate variables.

FIRST SIGN OF CHANGE: CORAL BLEACHING

Perhaps the most severe and wide-ranging impact of climate change on biological systems is coral bleaching. Corals have microscopic algae, zooxanthellae, that inhabit their cells in a symbiotic relationship. The algae photosynthesize and pass nutrients to the coral host and the coral provides a physical structure that protects the algae and keeps them in adequate sunlight for photosynthesis.

ZOOXANTHELLAE—THE OTHER HALF OF CORALS

Corals harbor microscopic algae called zooxanthellae within their tissues. Zooxanthellae provide products of photosynthesis to the coral, and the coral in turn provides a physical reef structure that keeps the zooxanthellae near the surface, where light for photosynthesis is abundant. When this symbiotic relationship breaks down owing to high water temperature, corals expel their zooxanthellae, causing them to appear white or "bleached."

However, when corals are exposed to high water temperatures, they expel their algae. Without the photosynthetic pigments in the zooxanthellae, the corals lose their color and all that is visible is their calcium carbonate skeleton, which appears white. The coral thus appears "bleached" (Figures 3.1 and 3.2). Coral bleaching was undescribed in the scientific literature 50 years ago, yet it is so common and widespread today that almost all coral reefs in the world have been affected at one time or another.

FIGURE 3.1 **Bleached coral.**
El Niño events in 1982–1983 and 1997–1998 bleached corals in reefs throughout the world. Bleaching is an increasingly common phenomenon even in non-El Niño years. This coral head in St. Croix bleached in 1995. *Source: Courtesy U.S. National Oceanic and Atmospheric Administration.*

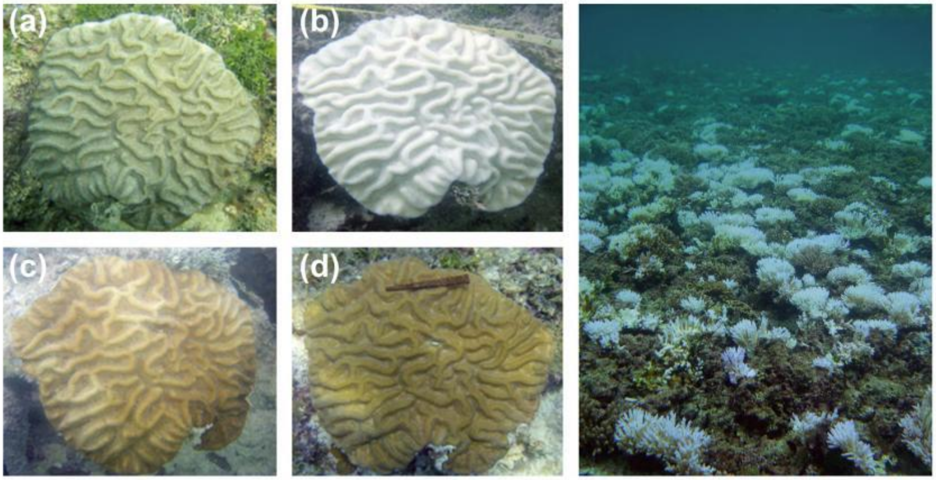


FIGURE 3.2 **1997–1998: A deadly year for corals.**
The right panel shows corals bleached in the El Niño event of 1997–1998. The left panels show a single coral head pre- and postbleaching: (a) prebleaching, (b) bleached coral head, (c) partially recovered coral head, and (d) fully recovered postbleaching. *Left Source: Manzello et al. (2007); Right Source: Courtesy U.S. National Oceanic and Atmospheric Administration.*

The intensification of coral bleaching is due to human-induced warming of the oceans. Corals live in the shallow surface waters of the ocean, which have warmed first and most quickly in response to atmospheric warming due to the greenhouse effect. As the atmosphere has warmed, some of that heat has been transferred to the surface of the ocean, resulting in warmed global mean ocean temperatures near the surface, or sea surface temperature (SST).

SEA SURFACE TEMPERATURE

SST drives many climatic phenomenon. SST is important because oceans comprise two-thirds of the Earth's surface and what happens at the air–water interface influences much of what happens near the habitable surface of the planet. SST is important in strengthening hurricanes and in determining the height of tropical cloud formations, among other phenomena. From disturbance regimes to cloud forest limits, change in SST is biologically relevant.

When these higher sea surface baseline temperatures are combined with warming in El Niño events, temperatures rise high enough for bleaching to happen. Bleaching occurs when SST rises more than 1 or 2 °C above normal summer maximal temperatures for periods longer than three to five weeks. Thus, both temperature and duration of exposure are important determinants of whether bleaching occurs and its severity once it happens. Because water temperatures vary between regions, the threshold temperature for bleaching is also different from region to region. It may also vary seasonally in the same region.

Once corals bleach, they often die. Recovery is possible but varies strongly depending on the severity of the bleaching event and conditions immediately after the event. Corals already weakened by other factors, such as pollution, sedimentation, or disturbance by tourism, are less likely to recover. For example, coral cover in the Great Barrier Reef in Australia declined 50% from 1985 to 2012 due to the combined effects of coral bleaching, cyclone damage and predation by crown-of-thorns starfish (*Acanthaster planci*).

Mortality due to bleaching may be severe enough to wipe out entire species over large areas. It is therefore a strong driver of range shifts in corals. For example, in the central lagoon of Belize, staghorn coral (*Acropora cervicornis*) was the dominant species until the 1980s, when it was wiped out by a combination of disease and rising water temperatures. The scroll-like coral *Agaricia tenuifolia* took over as the dominant coral, only to be wiped out in the high water temperatures of the 1998 El Niño event. These massive mortalities were the worst in at least 3000 years, resulting in range changes over large areas of the Caribbean for staghorn and other corals.

Reefs throughout the world are being hit with coral bleaching so severely that the future distribution of all tropical coral reefs is in question (Figure 3.3).

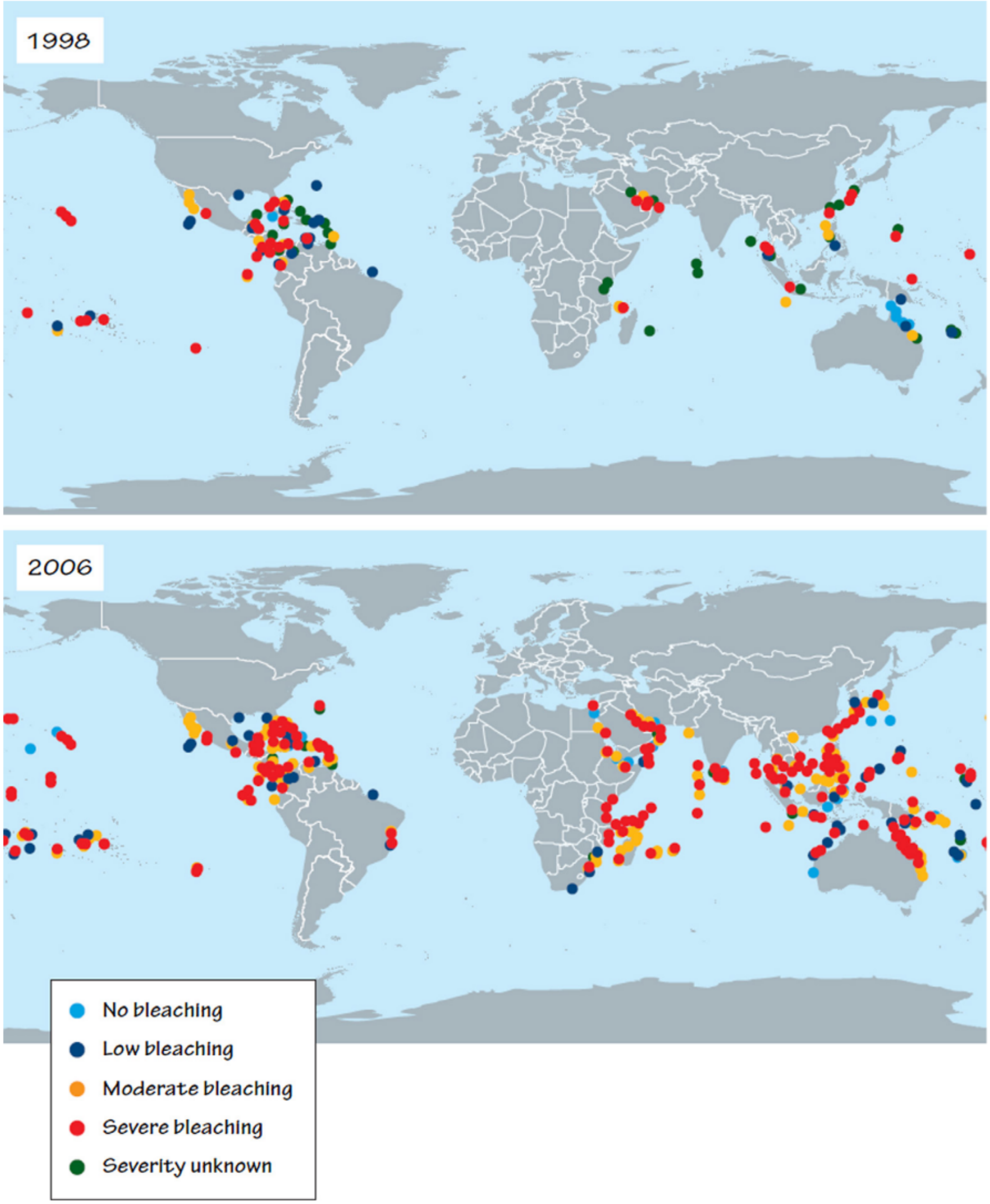


FIGURE 3.3 **Coral bleaching events.**
As global mean temperature rises, the frequency of events that exceed the bleaching threshold increases. The threshold varies in different regions. These global maps illustrate the severity of bleaching in the 1998 El Niño, which was the first major global bleaching event, and recorded bleaching in 2006. Every major coral reef region in the world has now suffered moderate to severe bleaching events. *Source: Marshall and Schuttenberg (2006).*

There were seven major coral bleaching events, affecting reefs in all areas of the world, between 1979 and 2002. There have been several panglobal mass bleaching events since. All of these events are associated with El Niño conditions. The 1997–1998 El Niño was the worst of the twentieth century for coral bleaching. In that event, reefs throughout the world were affected, many experiencing record damage. More than 10% of all the world's corals died in that event, with mortality in some regions, such as the Indian Ocean, as high as 46%.

These bleaching events are strongly affecting the regional distributions and density of virtually all types of reef-building corals. As in the Belize lagoon example, as population density crashes, species replacement may occur, resulting in range shifts (reductions) in the species most affected.

FIRST CHANGES ON LAND

A dramatic demonstration of a climate change-induced range shift from the terrestrial realm is provided by Edith's checkerspot butterfly. Checkerspot butterflies (genus *Euphydras*) had been known to be vulnerable to population crashes or booms owing to weather conditions for some time. A 1996 study showed that Edith's checkerspot butterfly (*Euphydras editha*) was undergoing a major range shift. The results were especially compelling because the study examined the entire range of the species—one of the first climate change and species' range shift studies to do so (Figures 3.4 and 3.5).

SPOTLIGHT: ADAPT, MOVE, OR DIE

Insects shed unique light onto past range shifts in response to climate change. Beetles currently known only from Asia are seen in the fossil record of the United Kingdom. Restricted-range endemic species that might have been interpreted as tightly evolved to local conditions are now known to have moved hundreds of kilometers or across continents on timescales of tens or hundreds of thousands of years. In many insects, affinity to climatic conditions seems to drive association with place rather than the other way around. Coope (2004) explores the implications of these findings for climate change biology and conservation. Coope suggests that a species faced with climate change has three options: adapt, move, or die. There is little evidence for extinction from the fossil insect record. An initial wave of extinction is seen at the onset of the ice ages, but once that spasm is past, few extinctions are associated with entry into, or emergence from, ice ages. One interpretation of this record is that the initial descent into glaciation eliminated species sensitive to major climatic shifts, and that remaining species are remarkably robust to change. There is even less evidence of adaptation in insects. One or two fossil beetle species seem to have arisen during the ice ages, but these seem not to have modern descendants, so they may represent adaptation or they may be anomalies. The final option, movement, is abundantly supported. Insect ranges moved long distances as the ice ages deepened and ebbed. Thus, for most of the world's species, moving in response to climate change seems to be a comfortable option. Whether it will remain so on a planet heavily altered by human action will determine the fate of millions of invertebrate species.

Source: Coope, G.R., 2004. Several million years of stability among insect species because of, or in spite of, ice age climatic instability? Philosophical Transactions of the Royal Society of London 359, 209–214.

Populations of Edith's checkerspot are found from Mexico to Canada, and populations in the south and in the lowlands were found to be disappearing faster than populations in the north and in the uplands. Continuation of this trend would lead to loss of lowland and southern range and an increase in range at upper elevations and poleward—exactly the pattern expected with climate change. Researchers were able to rule out competing causes for the shift, including habitat destruction, clearly indicating climate change as the cause of the range shift.

Since these early signs of range shifts, evidence has mounted for many species and many regions that climate change-caused range shifts are taking place.

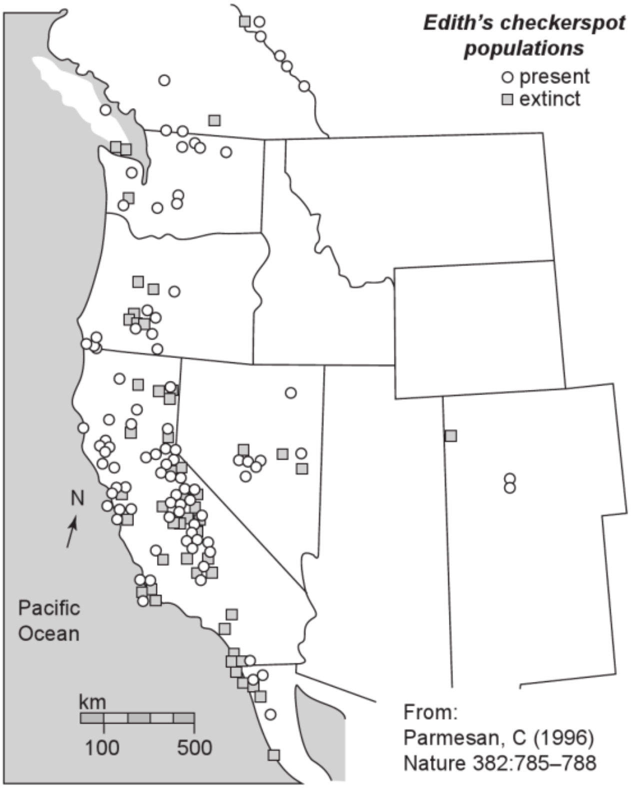


FIGURE 3.4 Edith's checkerspot butterfly range shift.
Southern populations of Edith's checkerspot butterfly are becoming extinct (shaded squares) more frequently than northern and montane populations, resulting in a northward and upslope range shift.
Source: Parmesan (1996). Reprinted with permission from Nature.

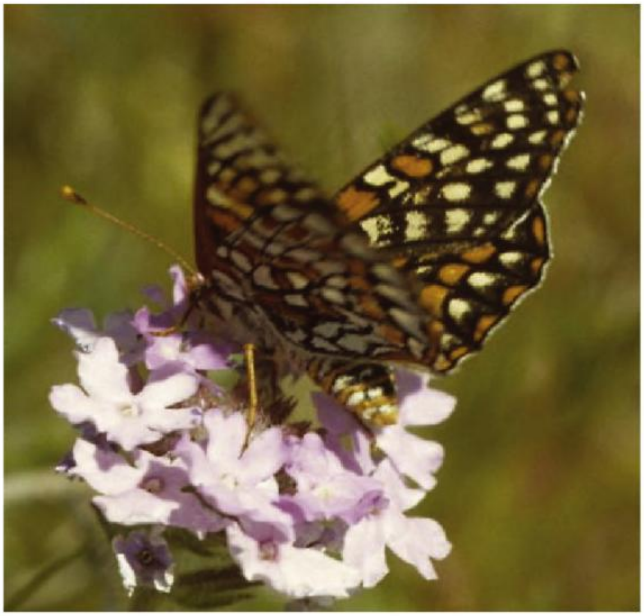


FIGURE 3.5 Edith's checkerspot butterfly (*Euphydryas editha*).
Source: From http://www.nps.gov/pinn/naturescience/butterfly.htm.

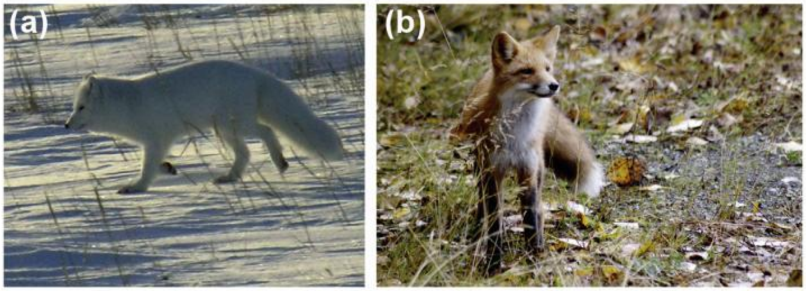
MOUNTING EVIDENCE OF RANGE SHIFTS

Evidence of climate change-related range shifts and population changes has accumulated rapidly since the pioneering marine and terrestrial studies in the 1990s. Evidence of impact is particularly strong for butterflies and birds, as well as for species at high latitudes. However, changes have been recorded in many taxa and across latitudes. Here, we survey some of the more important results, moving from the poles to the equator.

Arctic and Antarctic species have been particularly hard hit, as would be expected from temperature records and climate model simulations indicating that climate change will be more pronounced at high latitudes. Species dependent on sea ice have been selectively affected because of the large losses in sea ice extent that have occurred since 1970 (Figure 3.6).

The Arctic is rapidly losing sea ice, with severe impacts on species that depend on sea ice for some portion of their life cycle, such as polar bears, walrus and spectacled eider (see Chapter 5). Large-scale range changes have been seen in the arctic fox, which is retreating northward as its more competitive cousin, the red fox, expands its range with warming.

ARCTIC FOX AND RED FOX RANGE CHANGES



Arctic fox (a) and red fox (b).
Source: From (a) Wikimedia Commons and (b) U.S. Fish and Wildlife Service.

The arctic fox (*Vulpes lagopus*) is declining owing to climate change, in a range shift apparently mediated by competition with the related red fox (*Vulpes vulpes*). Arctic foxes have light coloration and compete well in snowbound landscapes. As climate warms, snow cover decreases and the advantages of this coloration for avoiding predators are lost. In these areas, the darker red fox is more competitive and pushes out the arctic fox. Thus, the range of the arctic fox is moving northward because of climate change, but the proximate cause is competition with the red fox.

FIGURE 3.6 **Penguins and climate change.**
Emperor penguin (*Aptenodytes forsteri*) populations are declining in Antarctica with climate change.
Source: Photo courtesy of NOAA. Photographer: Giuseppe Zibordi.

In the Antarctic, penguin ranges have shrunk and populations declined as sea ice has reduced in area. Emperor penguin populations have undergone population declines as high as 50%, and Adelie penguins have declined as much as 70% in some locations. Populations farthest from the pole have been hardest hit, as expected, creating the conditions for a poleward range shift in these Antarctic species.

Decreases in Antarctic sea ice have led to declines in the abundance of algae that grows on the underside of the ice and resultant declines and range retractions in krill that feed on the algae (Figures 3.7 and 3.8). Krill support fish, birds, and mammals higher in the food chain, so follow-on changes in the abundance and ranges of these species are expected, many of which are already being observed.

Acidification further influences the base of the polar food chain. Many plankton near the base of polar food chains form calcium carbonate shells. They do this in some of the coldest, and therefore least saturated, waters on the planet. Initially, warming of these waters may increase calcium carbonate saturation, pushing food web interactions in one direction. Later, direct acidification effects may provide pushback as increasingly acid polar waters become once again less hospitable to calcium carbonate-secreting organisms.

SPOTLIGHT: HIDDEN ADAPTATION

Although the "move" part of the adapt, move, or die trilogy is dominant, adaptation has occasionally been recorded (Thomas et al., 2001a). At the range margins of British insects on the move north in response to warming, long-winged variants are more common (Figures 3.9 and 3.10). This makes evolutionary sense because long-winged forms are better able to disperse to newly suitable climatic space than are short-winged forms, which often have very poor flight ability. However, where does this adaptation come from? Apparently, the long-winged trait is recessive. This allows it to persist in the gene pool with no ill effects because it is not expressed, despite being maladaptive when climates are stable and favorable. When climate changes, there is heavy selection for the ability to move to a suitable climate, and the recessive trait is expressed and selected for. These hidden traits are literally invisible until needed. When needed, they play a key role in climate adaptation.

Source: Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., et al., 2001a. Ecological and evolutionary processes at expanding range margins. Nature 411, 577–581.

In temperate climates, studies involving large numbers of species indicate broad biological response to climate change. In Europe, a study of 35 butterfly species found that 63% had undergone northward range shifts, as would be expected with global warming, and only 3% had shifted southward. In the species tracking climate, the range shifts were large—between 35 and 240 km. Similarly, in 59 species of birds in Great Britain, a mean northward range shift of nearly 20 km was observed over 20 years.

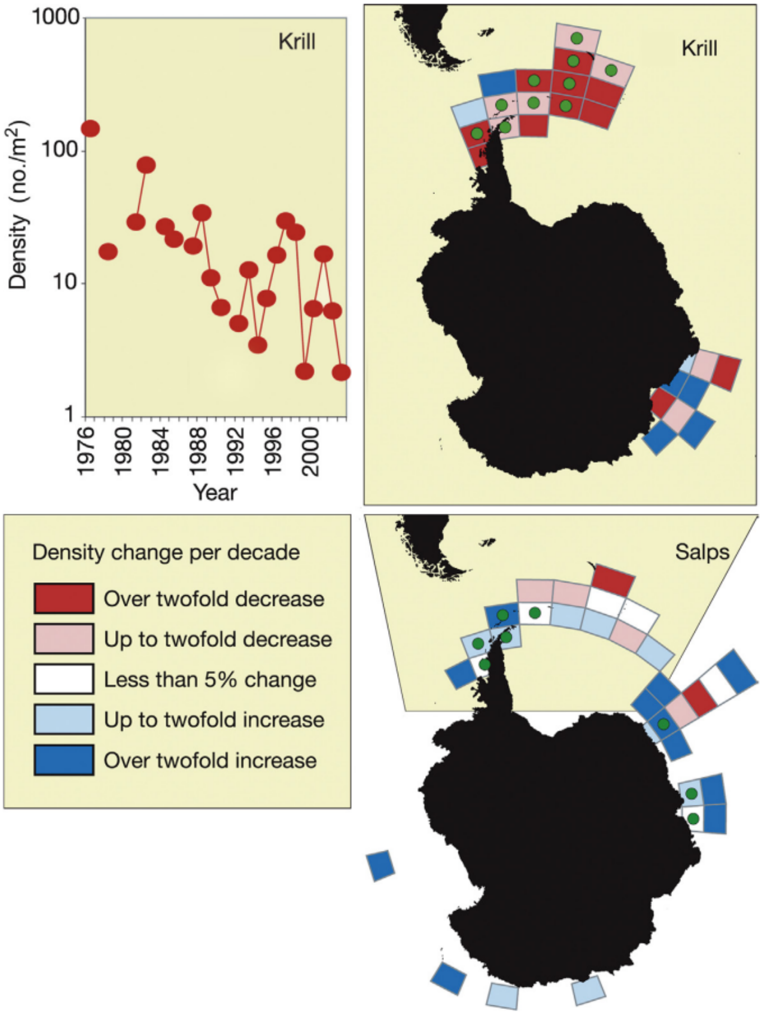


FIGURE 3.7 Shifting krill in Southern Oceans.

Krill abundance is decreasing in areas bordering Antarctica, whereas salp densities are increasing. Krill depend on ice algae for summer population growth. Declining sea ice due to climate change reduces algal density and depresses krill populations. Salps increase in their place. The maps show the change in krill (top) and salp (bottom) abundance. These changes have had profound impacts on food webs in the southern oceans. *Source: Atkinson et al. (2004). Reproduced with permission from Nature.*

Dragonflies in Great Britain have expanded northward; 23 of 24 well-documented species have shown a northward shift, with a mean shift of 88 km. A total of 77 lichen species have expanded their ranges northward into The Netherlands. Alpine plants have been moving upslope in Swiss mountains. In the United States, the pika (*Ochotona princeps*), a small montane mammal, is disappearing from lowland sites. These results are all for relatively well-known species for which

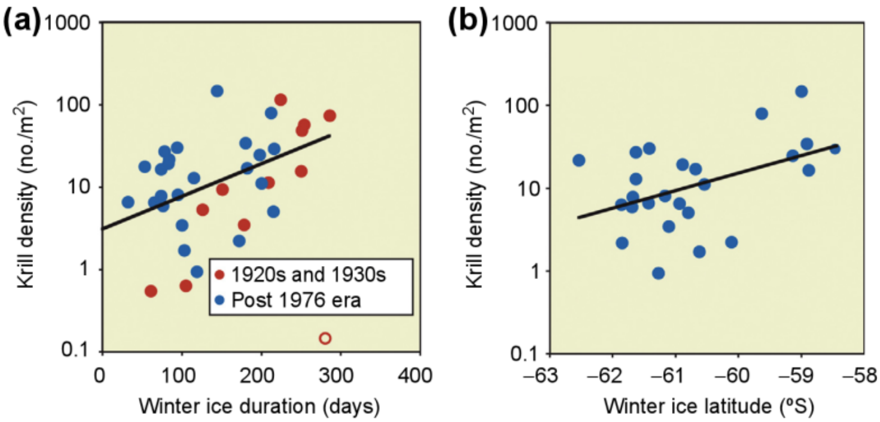


FIGURE 3.8 **Correlation between sea ice and krill density from region shown in Figure 3.7.**
Source: Atkinson et al. (2004). Reproduced with permission from Nature.

FIGURE 3.9 **The silver-spotted skipper (*Hesperia comma*) has expanded its range threefold in Britain since 1982.**
Source: Pimm (2001). Reproduced with permission from Nature.

good historical records exist. Butterflies and dragonflies are extensively collected by amateurs and professionals alike, whereas an avid bird-watching community generates exceptional amateur and professional sighting data, especially in Great Britain. Many other, less well-known species are likely to be shifting ranges in the temperate zone (Figures 3.9 and 3.10), and the number of documented cases is rising steadily, including invasions of nonnative species (Figure 3.11).

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Note: Page numbers followed by "f" indicate figures; "t" tables; "b" boxes.