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Marcia McNutt is Editor-in-Chief of *Science*.

Climate Change Impacts

ANTICIPATING THE FUTURE UNDER THE INFLUENCE OF CLIMATE CHANGE IS ONE OF THE MOST important challenges of our time, and the topic of the special section in this issue of *Science* (see p. 472). The natural systems that provide oxygen, clean water, food, storm and erosion protection, natural products, and the potential for future resources, such as new genetic stocks for cultivation, must be protected, not just because it is part of good stewardship but also so that they can take care of us. But even the first step of modeling the effects of greenhouse gas sources and sinks on future temperatures requires input from atmospheric scientists, oceanographers, ecologists, economists, policy analysts, and others. The problem is even more difficult because the very factors that influence temperature changes, such as ocean circulation and terrestrial ecosystem responses, will themselves be altered as the climate changes. With so many potential climate-sensitive factors to consider, scientists need ways to narrow down the range of possible environmental outcomes so that they know what specific problems to tackle.

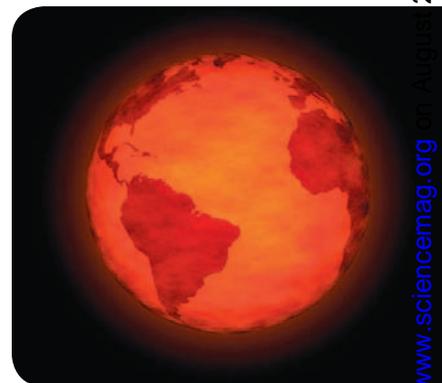
Researchers have turned to the geologic record to obtain ground truth about patterns of change for use in climate models. Information from prior epochs reveals evidence for conditions on Earth that might be analogs to a future world with more CO₂. Projections based on such previous evidence are still uncertain, because there is no perfect analog to current events in previous geologic epochs; however, even the most optimistic predictions are dire. For example, environmental changes brought on by climate changes will be too rapid for many species to adapt to, leading to widespread extinctions. Even species that might tolerate the new environment could nevertheless decline as the ecosystems on which they depend collapse. The oceans will become more stratified and less productive. If such ecosystem problems come to pass, the changes will affect humans in profound ways. The loss in ocean productivity will be detrimental for the 20% of the population that depends on the seas for nutrition. Crops will fail more regularly, especially on land at lower latitudes where food is in shortest supply. This unfavorable environmental state could last for many thousands of years as geologic processes slowly respond to the imbalances created by the release of the fossil carbon reservoir. The time scale for biodiversity to be restored, with all the benefits that it brings, will be even longer.

Unfortunately, I view these predicted outcomes as overly optimistic. We are not just experiencing increases in greenhouse gas emissions but also eutrophication, pollution of the air and water, massive land conversion, and many other insults, all of which will have interacting and accumulating effects. The real problem we need to solve in order to truly understand how Earth's environment may change is that of cumulative impacts. Although the Paleocene-Eocene Thermal Maximum (about 55 million years ago) is the time period considered to be a reasonable analog to a higher-CO₂ future, the planet was not experiencing these other stressors and climate change simultaneously. So terrestrial species that survive a climate impact alone may face extinction if reduced to a fraction of their natural range through deforestation and habitat fragmentation. Marine species that are mildly susceptible to ocean acidification may not be able to tolerate this condition plus low oxygen levels.

Sometimes the science of cumulative impacts is straightforward—for example, connecting habitats to provide migration corridors in response to sea-level rise brought on by climate change. But even “clear-cut” cases require extra work, more partnerships, and more time to address. Tackling problems of cumulative dimensions is a priority if we are to find viable solutions to the real environmental crises of the coming decades. There is a need for all scientists to rise to this challenge.

— Marcia McNutt

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INTRODUCTION

Once and Future Climate Change

ANTHROPOGENIC CLIMATE CHANGE IS NOW A PART OF OUR REALITY. EVEN THE MOST optimistic estimates of the effects of contemporary fossil fuel use suggest that mean global temperature will rise by a minimum of 2°C before the end of this century and that CO₂ emissions will affect climate for tens of thousands of years. A key goal of current research is to predict how these changes will affect global ecosystems and the human population that depends on them. This special section of *Science* focuses on the current state of knowledge about the effects of climate change on natural systems, with particular emphasis on how knowledge of the past is helping us to understand potential biological impacts and improve predictive power.

Four News stories focus on past and future impacts of climate change and the techniques that researchers are using to study them. Gibbons examines the role of climate variability in hominin evolution in Africa, and Pennisi profiles an effort to use sediment cores to document that variability. Kintisch explores whether coastal wetlands will be able to outclimb rising seas. And Pennisi offers a snapshot on the use of historical photographs to study climate impacts.

Four Reviews discuss recent research on the current and future effects of climate change as informed by our understanding of changing climates in the paleorecord. Diffenbaugh and Field review the physical conditions that are likely to shape the impacts of climate change on terrestrial ecosystems, showing that they will face rates of change unprecedented in the past 65 million years. Norris and colleagues review the Cenozoic history of oceanic change; despite some short-lived past analogs, the oceans will also experience more rapid change than ever before. Turning to ecology, Blois and colleagues discuss how climate changes can affect biotic interactions and how these insights might inform our understanding of future interactions. Moritz and Agudo discuss the prospects for species survival, weighing the evidence for persistence versus catastrophic decline.

Three Reviews focus on more specific impacts of climate change. Its influence on infectious disease is considered by Altizer and colleagues, who use examples from a wide range of host-pathogen systems to assess whether we are close to a predictive understanding of climate-disease interactions and their potential future shifts. Wheeler and von Braun assess the prospects for human food security, with particular attention to potential impacts on food supply in the world's more impoverished countries. Finally, Post and colleagues take a regional focus, reviewing the ecological consequences of current sea ice decline in the polar regions, the part of the world where the reality of changing climate is perhaps at its most stark.

— CAROLINE ASH, ELIZABETH CULOTTA, JULIA FAHRENKAMP-UPPENBRINK,
DAVID MALAKOFF, JESSE SMITH, ANDREW SUGDEN, SACHA VIGNIERI

Wet to dry. Kenya's Lake Magadi, now alkaline and mostly dry, once teemed with freshwater fish; a core drilled here will reveal ancient climate swings.

Natural Systems in Changing Climates

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Science



HUMAN EVOLUTION

How a Fickle Climate Made Us Human

Researchers are drilling for clues to how dramatic changes in African rainfall and vegetation shaped our species

Humans, like children, are the products of their environment. The famous anatomist Raymond Dart recognized that back in 1925, when he described the first hominin skull found in Africa. The evolution of this “Man-Ape,” he wrote, markedly differed from that of earlier apes. While apes lolled about in “luxuriant” tropical forests that posed relatively few survival challenges, the “Man-Ape” had to compete for scarce food and water with saber-tooth tigers and other dangerous beasts of the arid savanna—and ended up sapient. “For the production of man a different apprenticeship was needed to sharpen the wits and quicken the higher manifestations of intellect—a more open veldt country,” Dart wrote.

This “savanna hypothesis” suggested that as a drier climate caused grasslands to spread, our ancestors moved out of the trees and began walking upright in order to spot predators and prey in the waist-high stems. That freed their hands to use tools and spurred the development of big brains.

Today, no serious paleoanthropologist believes that particular evolutionary tale. But Dart’s hypothesis was the first of many to propose that shifts in climate and environment made humans who we

are. The idea has become practically received wisdom even though there has been little direct evidence to support or falsify it. True, researchers have extracted precise records of past climate from sea-floor sediments and ice cores. And they have noticed that fossils and environmental clues on land also suggest that some climate shifts coincide with changes in human ancestors.

But correlation is not causation, and only “a circumstantial case” has been made for climate as the engine driving human evolution, says paleoceanographer Peter deMenocal of Columbia University’s Lamont-Doherty Earth Observatory in Palisades, New York. Even correlation can be elusive: Syncing fossil discoveries with offshore climate records thousands of kilometers away has proven challenging. Most stories of how environmental change shaped our evolution have been “mainly fantasies of the past,” says paleoanthropologist Andrew Hill of Yale University. “They are not proven.”

That is beginning to change, however, as researchers deploy new tools to reconstruct climate and environment right where ancient hominins—the ancestors of humans but not other apes—once lived. This summer, for instance, a truck with a drilling rig has worked its way up the Rift Valley of Kenya, extracting sediment cores from dried-out lakebeds next to key fossil sites. Specialists are already analyzing a core drilled last year at Ologesailie in Kenya (see story, p. 476).

Wellsprings of data. Researchers are drilling deep into Africa's Great Rift Valley to get detailed climate data.

Such detailed, localized work may put some theories to rest and breathe new life into others, including a revived version of the savanna hypothesis.

“For the first time, we’ll be able to frame the question as: ‘How did hominins respond to the environment they lived in’ rather than as responses to global or Northern Hemisphere events,” says geologist Craig Feibel of Rutgers University in New Brunswick, New Jersey.

Grass roots

If the past is a foreign country, as historians say, then the pre-historic landscape is an alien world. Using a host of climate indicators, geologists have uncovered evidence of dramatic events that changed the planet in the past 7 million years, showing that the African landscape has evolved as dramatically as the anatomy of hominins. In the words of Dart, our ancestors’ “eyes saw, their ears heard, and their hands handled,” terrain far different from today’s.

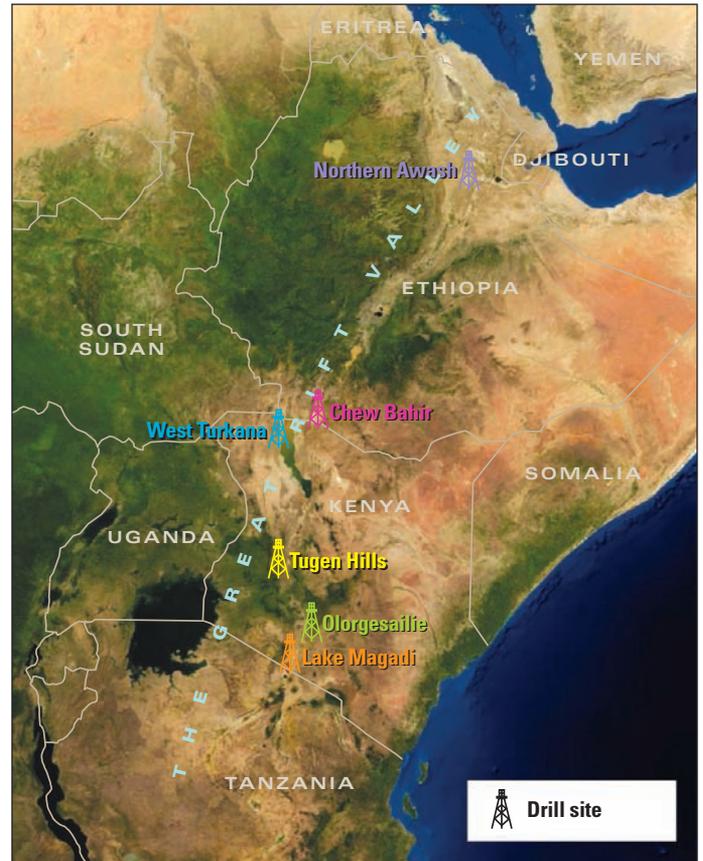
About 4 million years ago, for example, the Turkana Basin in Kenya—home to seven hominin species, including our direct ancestor *Homo erectus*—was covered by a vast inland sea, three times bigger than the lake there today. At the continent’s northern edge, the Mediterranean Sea dried up between 5 million and 6 million years ago, decreasing the circulation of moisture over Africa and Europe, according to a 2010 National Research Council report. This may have amplified a cooling and drying trend that had already started in Africa 6 million to 8 million years ago, according to oxygen isotopes from marine and ice cores.

That long-term drying trend, which began at about the time when the human and chimp lineages diverged, tempted some researchers in the 1990s to propose a revised savanna hypothesis: Drier, cooler climates thinned the forests of Africa, perhaps driving hominins out of the woods to scurry upright across open grasslands between patches of trees in search of food.

Then, new fossil discoveries challenged that idea. Paleoanthropologists found three very early, upright hominins that, according to clues left in the fossil sites, apparently lived in the woods between 7 million and 4 million years ago: *Ardipithecus ramidus* from Aramis, Ethiopia; *Orrorin tugenensis* from the Tugen Hills of Kenya; and *Sahelanthropus tchadensis* from Chad. For example, researchers found fossils of *Ar. ramidus* with fossilized wood and seeds, and near fossils of woodland monkeys, parrots, and snails. With hominins walking in the woods, the savanna hypothesis bit the dust.

Now, however, a half-dozen geologists are resurrecting the importance of grasslands in human evolution once again. This time, however, the theory has to do with how human ancestors used the savannas for food, not hunting and rambling.

The renewed savanna hypothesis has its roots in evidence that as African climate dried out 6 million to 8 million years ago, the makeup of plant communities was also shifting, says geochemist Thure Cerling of the University of Utah in Salt Lake City. That’s because the amount of carbon dioxide in the atmosphere began to decline 10 million years ago, giving a boost to plants that use the more efficient C_4 photosynthetic pathway; most of those plants are grasses and sedges, whereas woodland plants such as trees and shrubs usually rely on the older C_3 pathway. Grasses and other C_4 plants went from carrying out 1% of the photosynthesis in the tropics 10 million years ago to 50% today.



As went plants, so went the animals that grazed on them: By 6 million years ago, C_4 grasses had replaced C_3 plants as the most significant component in the diet of African grazers, Cerling says, according to studies of carbon isotopes in the tooth enamel of horses, elephants, antelopes, and other animals.

This suggests that hominins were born when grasses were on the rise. In fact, Cerling and his colleagues think that the first hominins had more grass in their environment than initially proposed—40% to 60% of the vegetation at nine *Ar. ramidus* fossil sites was C_4 plants, Cerling suggests (*Science*, 28 May 2010, p. 1105).

Recent data now show that later hominins responded to the rise of grasses by broadening their diets. Species that arose more than 4 million years ago, including *Ar. ramidus* and the oldest australopithecine, *Australopithecus anamensis*, subsisted on an apelike diet of at least 90% leaves and fruits from C_3 plants, Cerling and his colleagues reported in June in the *Proceedings of the National Academy of Sciences*. By 3.5 million years ago, a descendant of *Au. anamensis*—*Au. afarensis*, whose most famous member is the skeleton named Lucy—apparently adapted to the widespread grasslands by also munching on many C_4 plants, according to Cerling’s analysis of carbon isotopes in the tooth enamel of seven hominin species. *Au. afarensis*—a leading candidate for the ancestor of *Homo*—and another hominin, *Kenyanthropus platyops*, still ate mostly C_3 woodland plants, but about 22% of their diet was also made up of these C_4 plants, making them the hominins with the most varied menu. Their meals included grasses and sedges such as water chestnuts and papyrus and perhaps animals that fed on those plants.

This appetite for grasses apparently left its mark on *Australo-*



Where the hominins roamed?
New data suggest that grassland environments were important in hominin evolution.

Given that grasses were abundant in all hominin habitats for so long, “the savanna hypothesis is alive and well,” Cerling says. The grasslands may have had other evolutionary impacts, too, although the revived savanna hypothesis is so new that paleoanthropologists are just beginning to consider it. They note that the earliest hominins walked upright, but with a variety of odd gaits; the savanna may have favored adaptations for more effective walking and running, such as an arched foot and nonopposable big toe, that led to the typical human gait (*Science*, 11 February 2011, p. 750). “Cerling’s data are causing us to refocus on the link between environment and adaptation,” says paleoanthropologist Carol Ward of the University of Missouri, Columbia. “But we still have more questions than answers.”

pithecus anatomy: Most members of the genus had much larger molars and premolars than earlier hominins. Such big choppers would last longer than small ones when chewing on gritty grasses and abrasive sedges.

Dart’s savanna hypothesis,” says Richard Potts, a paleoanthropologist at the Smithsonian Institution in Washington, D.C. That’s partly because geologist Cerling uses a broader definition of “savanna” than many paleoanthropologists. But it’s also because the hominin most

Out of the Kenyan Mud, an Ancient Climate Record

MINNEAPOLIS, MINNESOTA—When Richard Potts, Anna Behrensmeyer, Alan Deino, and Richard Bernhart Owen get together, it’s usually at camp at Ologresailie in Kenya’s Great Rift Valley. The paleoscientists labor for hours in the hot sun, chipping away at exposed rock outcrops to develop a timeline for artifacts and other relics of the human ancestors who once lived nearby. But on a cold spring day earlier this year, they gathered with a dozen other researchers in a small lab at the University of Minnesota to analyze something quite different: 190 meters of mud, sand, and gravel cored last year, from what they hoped was once a lakebed 20 kilometers from their outcrops.

The team had never tried to drill a core before and hadn’t even known for sure that a lake ever covered the area. But as the researchers kicked off their “core sampling party,” they hoped that the mud would resolve into thousands of distinctive layers, each representing a different climate regime, ultimately reaching back 500,000 years. The goal: to test ideas about the role of climate variability in human evolution, by getting a continuous record of climate indicators from a place where hominins lived and died (see story p. 474). The project “has high potential to reconstruct the long-term history of environmental change,” says

team member Vanessa Gelorini, a paleoecologist at Ghent University in Belgium.

Although everyone eagerly anticipated what might be hidden in the 139 half-meter- to 3-meter-long cylinders of sediment, the group was anxious. The work required difficult on-the-spot decisions and taking hundreds of samples—chores best accomplished by everyone working together at the same place at the same time, says Potts, the Smithsonian Institution National Museum of Natural History (NMNH) paleoanthropologist who has led the Ologresailie project since 1986 and raised \$450,000 in private funding for the drilling and party. But cores don’t come with labels, and everyone had questions. Do we have a truly continuous record? How far back does it go? Can we date the layers? In other words, will this investment give us the data we seek?

Digging for climate proxies

At the field site, Ologresailie, researchers have been digging out artifacts and fossils since Louis and Mary Leakey first explored it in the 1940s. Since 1986, geologists have tried to extract clues to ancient climates from the outcrops (*Science* 23 March 1990, p. 1407). But the outcrops are not a continuous record of the past: They repre-

sent the period from 1.2 million to 500,000 years ago and then pick up again from 320,000 years ago to the present. Rock formed during the gap has eroded away.

Yet during those missing millennia, humans moved from a culture limited to stone axes to the so-called Middle Stone Age, marked by new tool innovations and perhaps more sophisticated social interactions. Potts proposed more than a decade ago that an increase in the variability of the climate during that time shaped human evolution by ratcheting up hominins’ genetic and phenotypic plasticity, so that they could survive in a broad range of conditions. Those changes prepared our ancestors to eventually spread worldwide.

But Potts’s theory couldn’t be tested without a climate record from the missing years. Where might it be preserved? One possibility was the Koor Valley 20 kilometers to the south, which was connected by a shallow depression to the Ologresailie site. Potts and his NMNH colleague Behrensmeyer speculated that sediments eroded away at Ologresailie had washed into the channel and down to the basin. If there had been a lake there, the researchers would be in luck. Lake bottoms typically accumulate sediments year after year, and, hidden from the sun and weather, those

specialized for the grasslands was not on the line leading to *Homo*. The “Nutcracker Man,” *Paranthropus boisei*, used its giant molars to crunch on a diet of 75% C₄ grasses and sedges, according to recent isotopic studies—and it died out about 1.2 million years ago, Lamont-Doherty’s deMenocal notes. They “weren’t the successful ones.”

Burst of speciation

Over the years, other hypotheses connecting human evolution to climate have also come and gone. For example, in the 1980s, Yale’s Elisabeth Vrba suggested that dramatic shifts toward a cooler, drier climate in the East African Rift Valley between 2.7 million and 2.5 million years ago sparked bursts of rapid extinction and speciation in grazers like antelopes, as well as in hominins. But this turnover-pulse hypothesis—so named because pulses of climate change were thought to spark big turnovers in species—faded after later studies showed that the shift in species happened more gradually. Still, the idea’s not dead yet: Arizona State University, Tempe, paleo-anthropologist Kaye Reed has spotted another burst of speciation about 3 million years ago at Hadar, Ethiopia. There, 10 new species, including camels and hoofed grazers, appear just before *H. habilis* replaced *Au. afarensis*.

Although Vrba thought that drying had sparked rapid speciation, other researchers have noticed that new species of hominins seem to appear during wet, humid periods. For example, studies of lake sediments in 10 East African rift basins suggested that the overall cooling and drying trend of the past 8 million years was interrupted by at least three humid periods when deep lakes filled, which tie in with the birth

of new hominins. So did cool, dry climates or wet, humid ones shape the evolution of hominins?

Potts has a different answer: It was all these changes, fluctuating wildly, that produced humans.

Creatures of change

Potts proposed 16 years ago that the key adaptation of the human lineage, manifested in everything from big brains to culture, is adaptability: Individuals who could survive in wet woods as well as dry grasslands fared better than those specialized for one or the other. He argues that the dramatic fluctuations of the ancient African climate shaped human nature, allowing our species to eventually thrive in all sorts of environments worldwide.

Deep-sea cores suggest that “the first appearance of every major genus in our evolutionary history, the origin of every major stone technology, happens to fall in long periods of high climate variability,” Potts says. He ticks off in rapid fire the innovations of such periods: the birth of *Australopithecus*, *H. habilis*, *H. erectus*, *Paranthropus*, and *H. sapiens*, plus the invention of the first stone tools 2.6 million years ago, the creation of more advanced Acheulean tool kits 1.8 million years ago, and the first Middle Stone Age technologies 300,000 years ago. Each event is correlated with a period of high climate variability, such as wet and dry cycles, Potts says. For example, the span between 2.5 million and 2.7 million years, which Vrba noted had such turnover in species, cycled between extremely wet and extremely dry times.

But the evidence for those fluctuations comes from predictions

sediments are often well-preserved. “We didn’t know for sure that there was going to be a lake,” Behrensmeyer recalls. “If it were just a pile of pumice or volcanic ash, it wouldn’t have preserved the environmental signals.”

To test the idea, Potts secured funding from several private foundations. A local drilling company spent September 2012 digging out two cores on the Koora Valley and shipped them here to the National Lacustrine Core Facility (LacCore), a lake core processing and storage lab supported by the U.S. National Science Foundation.

Guest of honor

At the core party, technicians begin slicing each 4-centimeter-wide core section lengthwise down the middle, enabling researchers to mine the sediment for a plethora of indicators of ancient climate. For example, different types of plants fractionate the two isotopes of carbon, C-12 and C-13, differently. So analyses of plant waxes extracted from the sediments can indicate whether dry-adapted grasses or moisture-loving vegetation thrived. Bits of calcium

carbonate, found in some soils, contain isotopes of oxygen (O-16 and O-18) that can reveal the temperature at which the carbonate formed. Certain clays indicate aridity.

Each material provides a proxy for what the environment was like during the formation of a sediment layer. Individually, however, the proxies and layers “are like blind men feeling the elephant,” Potts says. Only by combining them

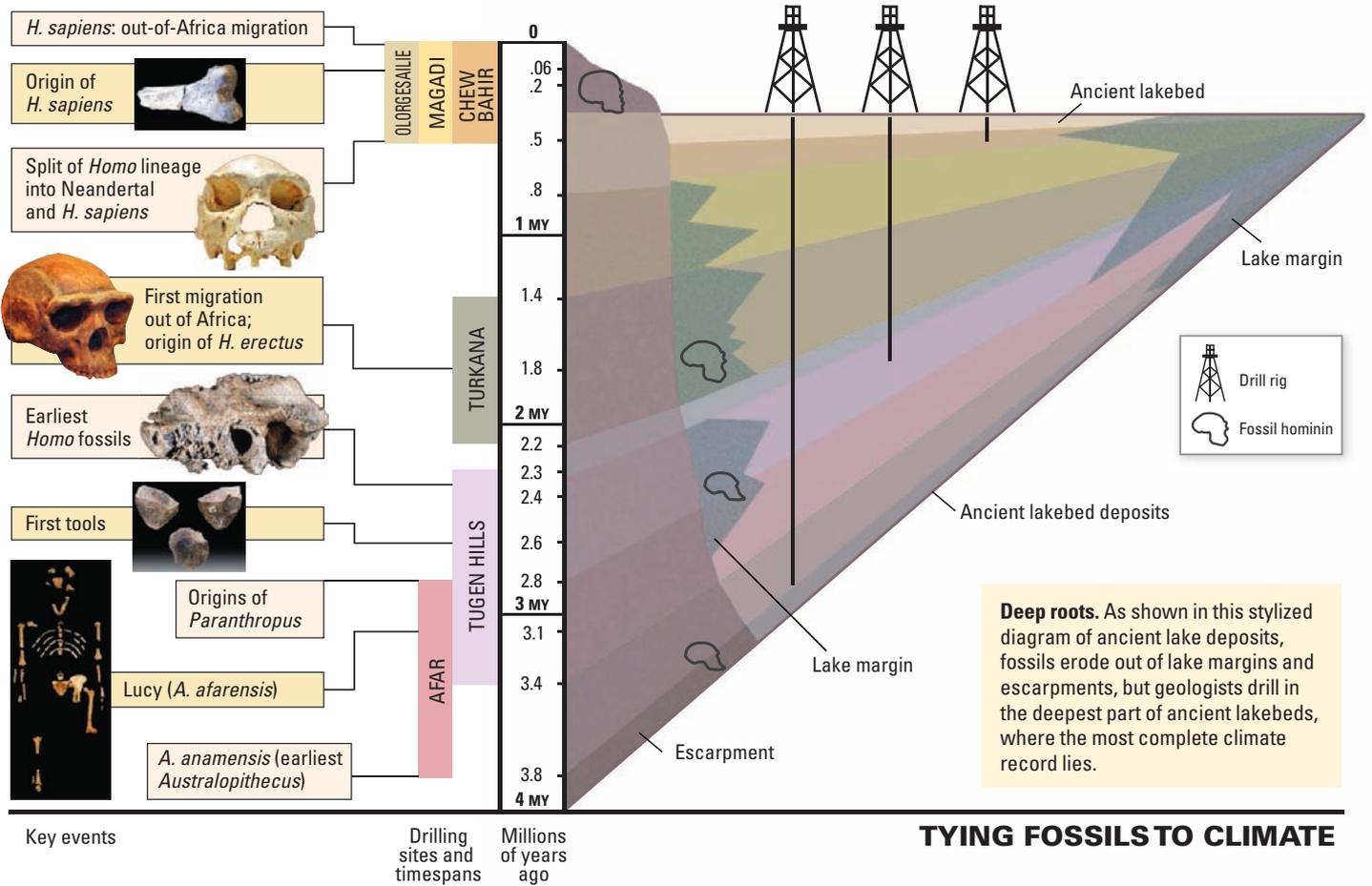
can researchers assemble a cohesive picture. And that depends on accurately dating the sediments. At this point, the team isn’t even sure that the core stretches to the sought-after 500,000 year time point. Dating is Deino’s job, and that’s why at this party he is the guest of honor. If he can find volcanic material, he can use radiometric dating to determine when it formed, and so provide a chronology for the cores, pegging the ups and downs of each climatic indicator to actual dates.

A beefy, taciturn geochronologist at the Berkeley Geochronology Center in California, Deino commands a dedicated computer terminal and one of the few stools in the lab—almost everyone else has to stand. He also gets first dibs on one-half of each sliced core. (The other halves are archived virtually untouched.)

The cutaways reveal a panoply of colors and textures, ranging from midnight black to sunrise yellow, from fine clay grains to small pebbles. In some sections the layered striations are so narrow that they are barely discernible by the naked eye. >>



Assembly line. In a week, Richard Potts, Anna Behrensmeyer, and their colleagues studied all the core’s sections.



Deino also receives color scans of each core, which he enlarges to search for dark areas that signal volcanic rock and ash. In one section known as 3A 4Q1, he pokes around with a metal spatula, exposing small, angular pieces of pumice. The angularity signals that these fragments are fresh from an eruption, rather than being deposited sometime after formation. They prompt a rare smile from Deino. He's taken dozens of samples, but none as promising as this one. "It's yelling 'Date me, date me,'" he says, digging out a chunk several centimeters long and scooping it into a bag.

Hours earlier, LacCore curator Anders Noren had urged the researchers to sample very conservatively, preserving as much core as possible for the future. But Deino takes as much as he wants, no questions asked, sometimes up to 300 grams at a time.

When Deino said he has "lots to look at," I breathed a huge sigh of relief," says team member Peter deMenocal, a geochemist at Columbia University's Lamont-Doherty Earth Observatory in Palisades, New York. Back at his lab, Deino will start by dating the best 10 samples that span the core from top to bottom, giving him a rough estimate of the overall sedimentation rate. Then he'll date more samples to boost the resolution. All other analyses will be pegged to the resulting chronology. "Al, all eyes are on you," deMenocal tells Deino.

Lake, or no lake?

Well, not all eyes. There's also the question of whether the sediment actually came from a lake, and so is likely to provide a continuous record. An initial look at the cores in the field suggested it had, but now came the real test.

Core up close. Digital images of split cores reveal details of the many layers, aiding the search for key environmental proxies.

Behrensmeyer and Owen, who has come all the way from Hong Kong Baptist University, hover over each core section to describe the texture, color, and layering. Such baseline data will help others know where to look for the climatic indicators they study.

Behrensmeyer studies enlarged photographs of the core for irregularities such as animal burrows or pieces of pumice, then pulls a dental pick from her hip pouch to tap the soil at those spots. Where the core seems to change character, René Dommain, a paleoecologist from the University of Greifswald in Germany, dissolves a tiny speck onto a slide and examines it with a petrographic microscope, whose polarizing filters help reveal the min-

from climate models and from marine sediments collected far from fossil sites. On the African continent, many local factors may have modified climate, such as rain shadows created by mountains or differences in altitude. Some basins may have been buffered from climate change and served as refugia.

The few cases where fossils are paired with local climate data offer tantalizing hints of support for Potts's idea. For example, layers of ancient sediment from outcrops in the Tugen Hills in Kenya reveal signs of wet and dry cycles, according to work by Yale's Hill and geologist John Kingston of Emory University in Atlanta. They collected diatoms, siliceous blue-green algae that grow in fresh water but vanish from sediments when a lake dries up. These tiny tracers mark when ancient lakes were full or dry, and showed that the Baringo Basin repeatedly filled and emptied every 20,000 years between 2.58 million and 2.69 million years ago. This was a response to cyclical changes in the orientation of Earth's axis as it orbits around the sun, the Milankovitch cycles, which in Africa create alternating wet and dry conditions. These cycles are the "pace-makers of African climate," deMenocal says.

The repeated shifts had a "kaleidoscopic" effect on animals in the basin, breaking up communities as the lakes filled, then allowing new mixes of species to reassemble when the lakes shrank, says Hill, whose team noted these shifts in fossils. One species that was part of the mix was *Homo*: The oldest *Homo* fossil was found just above a layer with diatoms, dating to 2.5 million years ago, suggesting that our genus arose just after the wet and dry cycles intensified in the Baringo Basin (*Science*, 4 February 2011, p. 540).

To nail down such links, however, researchers need local evidence, for example that climate changes preceded bursts of speciation, as predicted by the turnover-pulse hypothesis. The climate record near fossil outcrops is often incomplete. However, fine-scale evidence of such changes can come from the sediments that piled up

in the deepest part of ancient lakes, which trap chemical isotopes, pollen grains, charcoal, and other bits of detritus that offer telltale signs of past climates. "These lake sediments are like a metronome. They're accumulating all of the time," says paleolimnologist Andrew Cohen of the University of Arizona in Tucson. Adds Feibel: "Getting a lake record of environmental variability literally a few kilometers from the actual [hominin fossil] sites" can offer "an unprecedented perspective on when and how environmental fluctuations actually impacted these landscapes and habitats."

That's why this year, after 8 years of planning, an international team is drilling holes in six ancient lakebeds in Kenya and Ethiopia, says Cohen, who directs the \$5 million Hominin Sites and Paleolakes Drilling Project. In June, the group drilled down 228 meters and extracted cores in the Baringo Basin, hoping to sync the local wet-dry cycles with records from deep-sea cores, and to see local changes as early as 3.4 million years ago. Farther north, in the Awash valley, cores will test whether dry climate preceded the turnover in grazers 3 million years ago. If the cores don't show that climate changes intensified, the turnover-pulse hypothesis would be falsified in that lake basin. Conversely, if signs of grasses are common, the data may strengthen the revised savanna hypothesis.

The same drill rig is also taking cores from the habitats of other ancient hominins, including the site where a 1.6 million-year-old skeleton of *H. erectus* was found in the Lake Turkana Basin. The team also will core two lake basins in Ethiopia and Kenya that cover the time span drilled at Ologesailie—the past 500,000 years, when *H. sapiens* was born. "Each of these places will give us an interesting time slice through human evolution," Cohen says. The cores will enable researchers to "ask some of the most existential questions of our time," he says: "What it means to be human and what were the environmental constraints on why we are the way we are."

—ANN GIBBONS

eral composition of the smeared sediment.

The smear slides reveal little sign of life in the core's youngest, uppermost layers. Then a slide taken at 37 meters down is littered with diatoms, tiny algae with distinctive siliceous shells that grow in specific environments. "We have a lake," Owen announces to the group; they erupt into a cheer. Potts and Behrensmeier now know that their predictions are correct.

In subsequent slides, changes in the mix of diatoms reveal an ever-more saline environment as the

sediments get older. At about 44 meters down, diatoms peter out, perhaps indicating that the lake was temporary or too saline for diatoms. Dommain also records sightings of fossilized fungal spores, bits of other algae, phytoliths, charcoal, and pollen, all of which can record environmental dynamics. The presence of one colonial alga, *Botryococcus*, for example, indi-

cates a shallow lake. Charcoal speaks to fires: The bigger the piece, the closer the fire was to the lake. "All this [variability] tells you it's not a stable environment," Dommain says.

When the weeklong party finally breaks up, there is still plenty of work left. Over the next 18 months, the guests plan to complete their initial analyses and tie what they find to what they know from the outcrops. Ultimately, they'll develop a catalog of how the climate indicators changed over time, then attempt to model how climate changes affected the local ecosystem and the hominins who lived there. "We will have lots of stories" to tell, predicts Naomi Levin, a paleoecologist at Johns Hopkins University in Baltimore, Maryland. "But to figure out the importance for human evolution will take a lot more time."

—ELIZABETH PENNISI



Ready and waiting. At the LacCore lab in Minneapolis, 1.5-meter-long sections of core await processing.



Shovel ready. For conservationists in Rhode Island, restoring coastal marshes requires boots on the ground.

Wet benefit

Although they're not the most glamorous biomes, the United Nations estimates that wetlands are one of the world's most valuable providers of "ecosystem services," such as storm protection, water filtering, and seafood production. They also help lock up as much as 450 billion metric tons of carbon globally, absorbing warming compounds that might otherwise leak into the atmosphere.

Marshes have already experienced centuries of

WETLANDS

Can Coastal Marshes Rise Above It All?

As climate change causes sea level to rise, wetland scientists are struggling to predict which salt marshes will drown—and which might climb out of danger

WESTERLY, RHODE ISLAND—Biologist Marci Cole Ekberg plunges her shovel into a particularly gloppy spot in a mucky salt marsh near the Atlantic Ocean. Her goal: to drain one of many shallow pools that are creating dead zones in the expanse of otherwise dense grasses, a phenomenon that she's recently observed in more than a dozen other marshes around the state. She fears that the pools are an early consequence of the sea-level rise that is being driven by global warming and an ominous "glimpse of the future" for marshes in New England. Rising oceans will drown the grasses, she worries, eliminating rich habitats and leaving coastlines bare.

Other researchers, however, are skeptical that the pockmarks are a result of climate change, saying winter ice or other causes may be to blame. And Rhode Island isn't the only place where researchers are debating what is really happening in salt marshes today and how the wetlands will fare in a future of higher seas. There's wide agreement that these salt marshes are among the ecosystems most vulnerable to rapid sea-level rise. But few researchers are ready to predict the fate of specific marshes; there's still too much to learn, they say, about how wetlands in different regions accumulate sediments that might allow them to outclimb rising waters and whether they can escape by migrating inland.

Wetlands scientists are mobilizing to reduce the uncertainty. By building improved forecasting models and better monitoring systems—and studying wetland regions already experiencing dramatic sea-level rise—they're hoping to bring some clarity to a murky topic and identify practical steps to protect marshes. The overarching goal, says wetlands researcher Susan Adamowicz of the U.S. Fish and Wildlife Service in Wells, Maine, is to help managers "give marshes the best possible chance to outpace global sea-level rise."

insults—such as pollution, overfishing, and draining for farming and development—that have disrupted the ecological systems that help keep them healthy. Now, rising temperatures are causing land-based ice sheets to melt and seawater to expand. Such changes have already helped push sea level up by an average of 1.4 to 3.7 millimeters per year since 1950, according to a 2010 study published in *Science*. (Other estimates vary.) Climate models predict that the trend will accelerate to 1 centimeter or more per year as Earth continues to warm. And even a few extra centimeters of water can mean the difference between life and drowning for marshes, which typically occupy a narrow coastal band that ends just above the high tide line.

Faced with rising water, marshes have three options, says geologist Matthew Kirwan of the U.S. Geological Survey (USGS) in Charlottesville, Virginia: build in place by trapping and piling up new sediments, migrate to higher ground inland, or die. Predicting which path a marsh might take, however, requires understanding the interplay of a host of factors, including the biological traits of different marsh grasses and how wetlands construct muddy yet firm foundations from grains of sand, silt, and organic litter.

A sinking laboratory

To get a glimpse of how these factors might shape marsh adaptability in the future, researchers have begun to scrutinize one wetland ecosystem already experiencing local sea-level rise: Louisiana's Mississippi delta along the Gulf of Mexico. There, natural and human factors are causing the land to sink relatively quickly, creating a natural laboratory that simulates a sea-level rise of 1 to 2 cm per year. That could be "what it's going to be like everywhere by the end of the century," says ecologist James Morris of the University in South Carolina, Columbia.

Some delta marshes are adapting better than others: While grasses in a spot named Old Oyster Bayou have thrived, for instance, those in nearby Bayou Chitique have been largely submerged. The difference, researchers say, highlights the important role that an adequate sup-

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CREDIT: PETER HANNEY/SAVE THE BAY - NARRAGANSETT BAY

ply of fresh sediment can play in marsh survival. While Old Oyster Bayou receives some 70 mg of fresh sediment per liter of river water, allowing it to outclimb rising Gulf waters, Bayou Chitique's sediment infusions are largely blocked by upstream levees, reducing the load to just 20 mg per liter. The "natural process has been interrupted and there's not enough sediment," Morris says.

A 2010 modeling study that Kirwan and his USGS colleagues published in *Geophysical Research Letters* underscored the importance of sediment supply. In a scenario that included a rapid global sea-level rise of 1.25 m by 2100, the outlook for the 21st century was grim: "Most coastal wetlands worldwide will disappear," they concluded. But under slower scenarios, there was hope. Although marshes with low sediment availability fared poorly in the models, those with ample supplies often survived. A marsh's tidal range also played a role, the study found, with wetlands located in regions with larger gaps between low and high tide better situated to ride out sea-level rise, apparently because plants adapted for higher tidal ranges better withstand drowning.

Trench warfare

For conservationists, such studies suggest that it might be possible to help threatened wetlands adapt—for instance, by removing levees or dams to restore sediment, or even pumping in new mud. And in Rhode Island, the idea of ultimately aiding drowning marshes is what motivated Cole Ekberg, a biologist with the conservation group Save The Bay, to recently lug a shovel into a marsh here that is pockmarked with shallow grassless pools.

The origins and meaning of the pools is the subject of local debate, some fierce. Cole Ekberg and others say that their spread is a relatively recent development, documented in just the last few years in the higher-elevation parts of marshes in Rhode Island, Connecticut, Massachusetts, and Maine. And she's been running a restoration experiment of sorts, draining the pools to see if the grasses come back. "It's the best part of the day when water begins to move," she says.

Other marsh researchers are skeptical, blaming winter ice damage, invasive weeds, or geology. Mark Bertness, a marine ecologist at Brown University, sees "no evidence" of sea-level rise in the pools and says that the Save The Bay staff members are "well-intentioned but naive."

Bertness also wonders whether the focus on sea-level rise is diverting attention from more immediate threats. His own studies, for instance, have shown that overfishing has resulted in a boom in a population of crabs that chow on marsh grass, sometimes causing severe damage. "I was just dumbfounded what these crabs have done over a 2, 3-year period," he says. "Sea-level rise is going to come along, but this is happening now."

No escape route

All sides, however, appear to agree that if a marsh doesn't have a sediment source that will allow it to build up, "then the question becomes will it be able to migrate," Kirwan says.

Increasingly, the answer is no. Marshes around the world are hemmed in by development that essentially blocks migration

to higher ground. In many areas, the obstacles are concrete or stone sea walls built to protect seaside homes or industrial sites. In Europe and parts of Asia, studies have found that two-thirds or more of many shorelines have been "armored." Even sparsely populated sites can leave marshes little room: A 2000 study of Maine's lightly inhabited Casco Bay found that one-fifth of its shoreline was armored.

Some researchers are beginning to look at ways to clear such obstacles. Around the Blackwater National Wildlife Refuge near Maryland's Chesapeake Bay, for instance, a coalition of conservation and government groups has embarked on an ambitious effort to identify potential obstacles and protect possible migration paths. The group is even eyeing pine forests and farm fields that may have the right topography and soil types to be converted to future marshes. The Nature Conservancy has launched a similar effort on Long Island in New York state, while Rhode Island officials, scientists, and activists are working on a statewide assessment to map out risks to wetlands under different scenarios.

It could take decades to realize such forward-thinking efforts, planners say. In the meantime, scientists say that they need better ways to monitor how marshes are doing now. A good start, a team of USGS researchers argued in an April paper in *Nature Climate Change*, would be to create a global

Bayou blues. Louisiana's disappearing marshes offer a glimpse of how global wetlands may respond to rising seas.



network of 14,000 relatively simple devices called surface elevation table markers. Secured to the ground beneath marshes, mangroves, and wetlands, they can register changes in the height of the marsh surface to an accuracy of 0.01 cm, more precise than surveys, LiDAR, or satellite readings. The authors say the network, which might cost \$8 million to create, "would allow policymakers to prioritize wetland sites for intervention."

That's a goal that Save The Bay's Cole Ekberg supports. "Someone might ask what's the point of protecting salt marshes anyway, if they're doomed in the long run," she says. "My answer is if we can extend their lives 20 or 30 years, it's a valuable investment."

—ELI KINTISCH



GEOGRAPHY

Worth a Thousand Words

Models and experiments only go so far in assessing the effects of climate change. For a reality check, researchers turn to historical photos

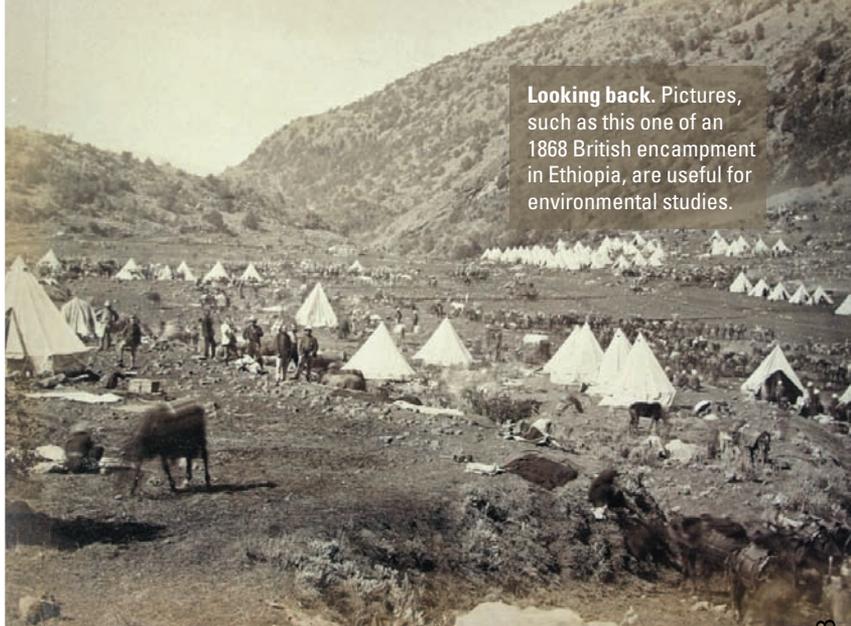
In 1868, British soldiers lugged a 500-kilogram camera into the Ethiopian mountains—not to shoot snapshots, but to photocopy documents for headquarters. Occasionally, however, they trained the lens on their surroundings. Now, 145 years later, the antique photos provide a unique window into how climate change and other factors have affected Ethiopian ecosystems. By comparing the historic images with modern photos snapped at the very same spots, researchers are documenting biological shifts that might be otherwise invisible. And Ethiopia isn't the only locale captured in historic photographs: Researchers have also turned up valuable troves from China and the Arctic. The photographs represent “a very powerful ecological tool,” says Isla Myers-Smith, an ecologist at the University of Edinburgh in the United Kingdom.

Although repeat photographs of receding glaciers yield perhaps the most iconic images of climate change, before-and-after images also

document more subtle biological shifts. Changes in forest or desert cover, acceleration of plant growth, and shifts in species can all show up. Realizing the potential of repeat photography, however, isn't easy.

First, researchers must track down potentially useful historic images. Most photos dating back a century or more were taken for reasons other than documenting the environment, so just a handful may be relevant to, for instance, climate change. “You can do a lot of looking,” Myers-Smith says. Then, scientists need to find out where the picture was taken and make the effort to return to the site. That may mean “hours of walking around looking for the ‘right’ bend in the stream or bump on the ridge,” she says.

But the effort can be worth it. Photo comparisons have yielded numerous insights and a few surprises. In these pages, *Science* takes a look at a few projects that use photos to go back in time.



Looking back. Pictures, such as this one of an 1868 British encampment in Ethiopia, are useful for environmental studies.

Advancing Seasons in China

Repeat photography was a labor of love for Yin Kaipu. In 2004, at age 60, the botanist from the Chengdu Institute of Biology in China, decided to follow in the footsteps of American plant collector Ernest H. Wilson. At the turn of the 20th century, camera in tow, Wilson explored western China for Harvard University's Arnold Arboretum. Much later, Yin covered some of the same territory for his work and was excited to recognize places where Wilson had taken photographs. “The landscape that I saw had already gone through great change since Wilson's time,” Yin says.

It took him 7 years to gather 1000 of the historical photos, 400 of which had potentially telltale landmarks. Based on books that traced Wilson's travel routes, Yin plotted a course through the 753,300 square kilometers of Sichuan, Hubei, and Chongqing provinces. He estimated that, in advance, he could pinpoint each location to within 30 kilometers.

Six years later—after raising \$200,000; traveling on foot, horseback, motorcycle, and boat; and pushing his body to its limits—



1910

Yin had documented severe deterioration of the natural environment and a reduction in biodiversity, he says. The photos revealed climate change impacts as well. In one county, for instance, farmers plant rice a month earlier than they did 100 years ago. Elsewhere, the dates on the early and recent images showed

that a spring flower, *Primula*, also blooms a month early.

Yin is not the only repeat photographer combing China's landscapes. Conservation biologist Robert Moseley was exposed to the technique as an undergraduate in the 1970s, during a summer job in Idaho documenting

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2008



1868



Humans Greening A Landscape

The camera the British army sent to northern Ethiopia in 1868 captured 30 landscape photos that were of interest to Jan Nyssen, a geographer now at Ghent University in Belgium. They've proved unusually valuable, given the scant historical information about vegetation, terrain, and land use in the region.

All told, Nyssen has now amassed historical photos of Ethiopia from about 20 sources, spanning 1867 to the present. He's been able to create some 500 then-and-now pairs and has been surprised by some of the differences they show. With population increases and climate changes, he and others expected the landscape to become degraded and more desertlike over time. But many sites have more trees and shrubbery now than when the

Greening trend. A dry Ethiopian landscape has since sprouted more trees, thanks in part to conservation efforts.

British marched through this mountainous region, he says.

The trend toward a richer landscape was not consistent, however. The photos suggest an increase in vegetation through the 1930s, then a degrading landscape into the 1970s, with severe desertification between 1975 and 1984. Since then, there appears to have been a gradual improvement as the government and individual landowners have become more conservation and management-oriented. So far, Nyssen says, "most changes

are related to direct human intervention and that's overriding climate change." Still, the photos should have "relevance" for studying climate change, he adds, as global warming takes hold.

—ELIZABETH PENNISI



REVIEW

Changes in Ecologically Critical Terrestrial Climate Conditions

Noah S. Diffenbaugh^{1,2*} and Christopher B. Field³

Terrestrial ecosystems have encountered substantial warming over the past century, with temperatures increasing about twice as rapidly over land as over the oceans. Here, we review the likelihood of continued changes in terrestrial climate, including analyses of the Coupled Model Intercomparison Project global climate model ensemble. Inertia toward continued emissions creates potential 21st-century global warming that is comparable in magnitude to that of the largest global changes in the past 65 million years but is orders of magnitude more rapid. The rate of warming implies a velocity of climate change and required range shifts of up to several kilometers per year, raising the prospect of daunting challenges for ecosystems, especially in the context of extensive land use and degradation, changes in frequency and severity of extreme events, and interactions with other stresses.

Even before biogeographic relationships between vegetation and climate were described by von Humboldt (1), every traveler had the opportunity to see climatic controls on ecosystems expressed on every mountain range and across continents. Indeed, the earliest evidence for past climate changes came from mismatches between the current and fossil distributions of plants and animals. Some of the observed range shifts were hundreds or thousands of kilometers, a vagility that might be relevant to future migrations. But is it really? Individuals and species can potentially respond to changes in climate through a variety of pathways, including migration in space that allows persistence of the current climate conditions in a new geographic range and behavioral and/or evolutionary adaptations that allow persistence of the current geographic range in the face of new climate conditions (2). However, failure to respond sufficiently rapidly can result in species extinction (2, 3).

The sensitivity of plants, animals, and ecosystems to climate and climate-related processes is broadly documented (4–7). Evidence for this sensitivity arises from the patterns expressed on the current landscape; observations of recent, historical, and fossil range shifts; results of manipulative experiments; and inferences based on empirical and process models (2). However, despite this body of evidence, a number of complexities pose important challenges to impact assessment, including the dispersal ability of different taxa (8), the evolutionary response of

individual species (9, 10), the ecological response to novel climates (11–14), and the potential for climate “refugia” within the current geographic range (15). Further, species and ecosystems will encounter not only a range of climate conditions that is potentially different from any in the past but also the broader conditions of the Anthropocene (16), in which human actions either dominate or strongly influence a wide range of Earth system processes (17). The impacts of climate change will therefore result from interactions with other stresses, such as land use change, biological invasives, and air and water pollution (17–19). Recognizing the potential importance and limited understanding of physical climate changes; the behavioral, evolutionary, and ecological responses to those changes; and other interacting stresses can provide a starting point for managing evolving risks (20, 21).

Since the beginning of the 20th century, global mean temperature has increased by $\sim 0.8^\circ\text{C}$ and has been accompanied by rising sea level, altered seasonality, and changes in extremes (22). Since 1979, surface air temperatures over land have increased at about twice the rate of temperatures over oceans (23). It is very likely that warming will continue, with the magnitude determined by a combination of intrinsic features of the Earth system and human actions (22, 24).

Assessment of possible future changes in ecologically critical climate conditions requires three different kinds of information. First is an understanding of the aspects of climate change that drive biological response. Second is a comparison of current and future climate change with examples from the past, including both the magnitude and rate of change. Third is a picture of the context in which current climate change is occurring, and the consequences of that context in structuring constraints and opportunities. We

address all three elements, emphasizing the physical climate.

Projected Climate Change over the 21st Century

The trajectory of climate over the 21st century depends on three classes of factors: (i) the energy imbalance already built into the system as a result of past forcing by greenhouse gases (GHGs) and other changes (25); (ii) the intrinsic sensitivity of the climate system to anthropogenic forcing (26), including atmospheric, carbon-cycle, and other feedbacks (27); and (iii) the magnitude of future forcing, such as by GHGs and aerosols not yet released (28). Analyses of observed trends and geologic records provide critical insights for the first two kinds of factors, but uncertainties about the rate and pathway of future emissions create a need for controlled experiments that can account for potential thresholds, feedbacks, and nonlinearities. Because such experiments cannot be run on the real global system, climate models are used to explore possible futures.

Phase 5 of the Coupled Model Intercomparison Project (CMIP5) includes contributions from 25 modeling centers, using models with multiple structures, parameterizations, and realizations within a given forcing pathway (29). Climate forcings are provided by Representative Concentration Pathways (RCPs), which characterize the most important features of feasible alternative futures and are designed to be consistent with physical, demographic, economic, and social constraints (28, 30). The RCPs, like the Special Report on Emissions Scenarios (SRES) (31) and other earlier scenarios, are not intended as predictions and are not assigned probabilities or other indicators of expectation. Each RCP reaches a different level of anthropogenic radiative forcing in 2100, ranging from 2.6 W/m^2 for RCP2.6 to 8.5 W/m^2 for RCP8.5.

We discuss simulation results for the full range of RCPs, but with more examples from RCP8.5 because actual emissions since 2000 have been closest to RCP8.5 (32) and RCP8.5 spans the full range of 21st-century forcing encompassed by the RCPs (33). For the next few decades, when historical warming will be maintained by emissions that have already occurred (34–36) and when any investments in mitigation will still be building momentum, differences across the RCPs are small (33). The latter decades of the 21st century are really the era of climate options, in which differences in emissions—including in the near term—have potentially large consequences for climate.

For RCP8.5, the CMIP5 ensemble exhibits substantial warming over all terrestrial regions by the 2046–2065 period (Fig. 1) (37). The largest annual warming occurs over the Northern Hemisphere high latitudes, including $>4^\circ\text{C}$ above the 1986–2005 baseline (or about 5°C above pre-

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industrial temperatures) (Fig. 1) (22). Annual warming exceeds 2°C over most of the remaining land area in 2046–2065, including greater than 3°C over large areas of North America and Eurasia. By 2081–2100, warming exceeds 4°C over most land areas, with much of northern North America and northern Eurasia exceeding 6°C. The CMIP5 pattern of mean

warming is consistent between intermediate and high levels of forcing, as was the case with CMIP3 (38).

Substantial changes in annual precipitation emerge over some areas by 2046–2065 in RCP8.5, including increases over the high northern latitudes and decreases over the Mediterranean region and the mediterranean-climate regions of

southwestern South America, Africa, and Australia (Fig. 1). These patterns intensify by 2081–2100. The comparison between the 2046–2065 and 2081–2100 periods of RCP8.5 suggests the persistence of some regions that become drier and some that become wetter, with spatially durable patterns that increase in magnitude in response to increased forcing.

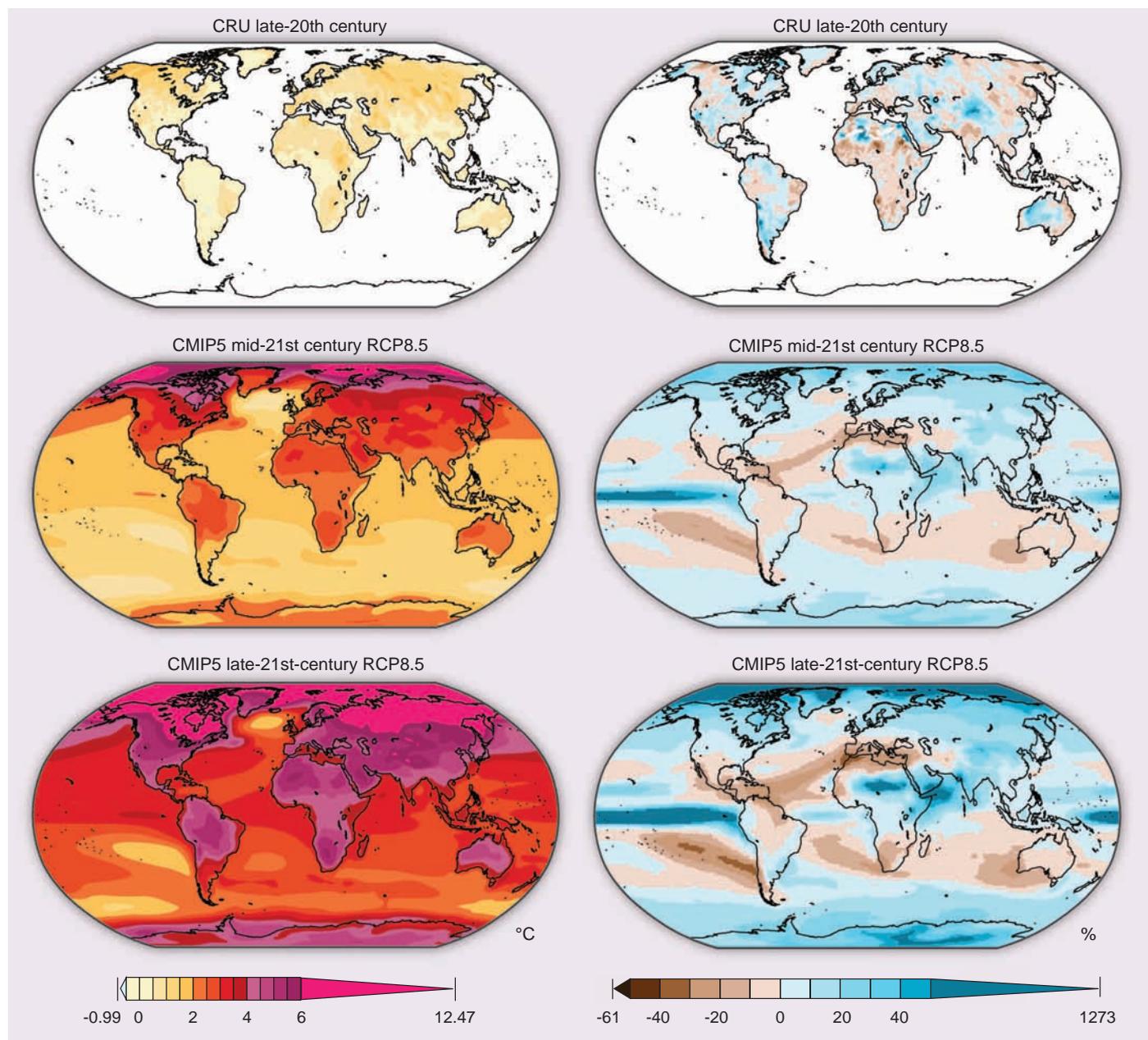


Fig. 1. Observed and projected changes in annual temperature and precipitation. (Top) Climatic Research Unit (CRU) observations (which are available only over land), calculated as 1986–2005 minus 1956–1975. (Middle) Differences in the mid-21st-century period of the CMIP5 RCP8.5 ensemble, calculated as 2046–2065 minus 1986–2005. (Bottom) Differences in the late-21st-century period of the CMIP5 RCP8.5 ensemble, calculated as 2081–2100 minus 1986–2005. We show the multi-model mean, using the model aggregation of Diffenbaugh and Giorgi (65). This presentation does not

indicate significant differences from background variability, nor does it reflect many other potentially important sources of uncertainty, including level of emissions, Earth system feedbacks, or model structure. The values at the left and right extremes of the color bars give the minimum and maximum values (respectively) that occur across all of the periods. The minimum temperature, minimum precipitation, and maximum precipitation extreme changes are all in the CRU observations. Further details are provided in the supplementary materials.



Climate Extremes

Sensitivity to climate extremes can be found in tropical, temperate, and boreal ecosystems. For example, tree mortality in the Amazon has been linked to drought (39–41), severe heat (42), and extreme wind (43). Drought and human-induced biomass burning and deforestation (44–46) combine to increase tropical forest fires—and loss of tropical forest cover—during strong El Niño events. Temperate ecosystems experience forest die-off (47–49) and decreased primary production (50) in response to severe heat and drought, with low spring and summer snowmelt runoff increasing stress on mountain, riparian, and dry-land ecosystems (51–54) through increased pest pressure (55), wildfires (52), and decreased water supply for riparian and montane ecosystems (51, 56, 57). In the Arctic, extreme winter warm events can cause vegetation damage and reduced summer growth (58), alteration of community composition (59), and changes in microbial habitats (including loss of ice and thawing of permafrost) (60), whereas drought and temperature stress can limit boreal forest growth and carbon uptake (61–63).

A large body of literature, assessed in the 2012 Intergovernmental Panel on Climate Change (IPCC) *Special Report on Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation* (64), indicates that further global warming is likely to alter the occurrence, severity, and/or spatial pattern of a number of different types of climate extremes. CMIP5 projects substantial increases in the occurrence of extreme hot seasons in both RCP4.5 and RCP8.5 (65), with most land areas experiencing >50% of years with mean summer temperature above the late-20th-century maximum by 2046–2065 in RCP8.5, and >80% of years by 2080–2099 (Fig. 2) (65). These same projections include increases in the frequency of extremely dry seasons by 2080–2099, with areas of Central America, northeastern South America, the Mediterranean, West Africa, southern Africa, and southwestern Australia all exhibiting >30% of years with mean seasonal precipitation below the late-20th-century minimum (Fig. 2) (65). The occurrence of extremely low spring snow accumulation is also projected to increase in

much of the Northern Hemisphere, including >80% of years below the baseline minimum over areas of western North America by 2080–2099 (Fig. 2) (66).

A number of daily-scale extremes are also projected to change in response to elevated GHG forcing (64). For RCP8.5, CMIP5 simulates statistically significant increases in the occurrence of daily-scale hot extremes over all land areas and in the occurrence of extreme daily-scale wet events over most land areas (excepting the areas of robust drying seen in our Fig. 1) (67). Climate model experiments also project the hydrologic intensity—as measured by the combination of daily-scale precipitation intensity and dry spell length—to increase over almost all land areas in response to continued global warming (68). Further, the occurrence of

frost days and severe cold events, which can be critical for limiting the ranges of a number of species [including some pests (69)], decrease in response to further global warming (67, 70, 71). The greatest uncertainties in daily-scale extremes are associated with severe storms such as tropical cyclones and tornadoes, which exhibit complex physical dynamics and incomplete observational records (72–76).

Some changes in extremes already have been observed (64). For example, the fraction of land area experiencing extreme seasonal heat has increased over the past three decades, both globally and over most tropical and some mid-latitude land regions (Fig. 2) (77). The intensity, occurrence, and duration of heat waves have likewise increased globally (78), where—as the occurrence of daily-scale cold extremes

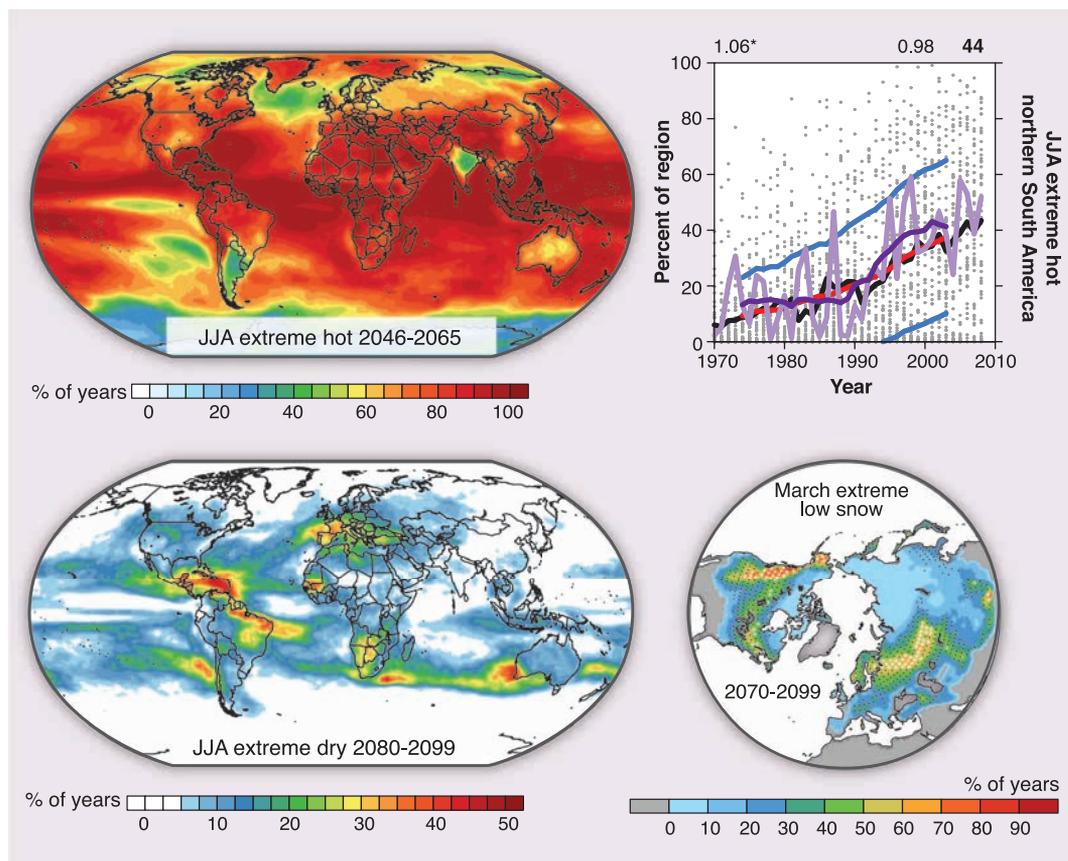


Fig. 2. Changes in seasonal extremes. (Left) The frequency of the 1986–2005 maximum June–July–August (JJA) temperature (top left) and minimum JJA precipitation (bottom left) in the 2046–2065 and 2080–2099 periods of RCP8.5 [from (65)]. (Bottom right) The frequency of the 1976–2005 minimum March snow water equivalent in the 2070–2099 period of RCP8.5, with black (white) stippling indicating areas where the multimodel mean exceeds 1.0 (2.0) SD of the multimodel spread [from (66)]. (Top right) The fraction of land grid points in northern South America with JJA surface air temperatures above the respective 1952–1969 maximum [from (77)]. The light and dark purple show the annual and 10-year running mean of the observational time series, with the trend shown in the top left (percent of region per year; asterisk indicates statistical significance). The gray points show each CMIP3 realization, the black and red show the annual and 10-year running mean, and the blue shows a 1-SD range. The mean of the trends in the CMIP3 realizations is shown in the top right, with the number of realizations (out of 52) that exhibit a statistically significant trend shown in bold. Further details are provided in the supplementary materials.

has decreased globally and over most extra-tropical land areas (79). The occurrence of extreme wet events has also increased globally (80), although not all regions exhibit uniformly increasing trends (81). Last, droughts have increased in length or intensity in some regions (64), and the hydrologic intensity has increased over many land areas (although the observed signal is less uniform than the simulated response to further global warming) (68).

A Range of Possible Futures

A key source of uncertainty for ecosystem impacts is the magnitude of climate change that ecosystems will encounter in the coming decades. Multiple factors contribute to this uncertainty, including the magnitude of global-scale feedbacks [such as from clouds (82) and the carbon cycle (83)], the response of certain extreme events to elevated forcing (72, 73), and the influence of internal climate variability on the local climate trend (84). The level of GHG emissions from human activities is, however, the largest source of uncertainty in the magnitude of global climate change on the century time scale (27, 85, 86), with uncertainties about physical climate mechanisms contributing a progressively larger fraction of uncertainty at smaller spatial and temporal scales (87).

The feasible range of human GHG emissions is very large (Fig. 3) (30, 88–94). The RCPs span a range from less than 450 parts per million (ppm) carbon dioxide (CO₂) for RCP2.6 to

greater than 925 ppm in 2100 for RCP8.5 (Fig. 3) (30). Although RCP2.6 is considered technically feasible, it requires economy-wide negative emissions in the second half of the 21st century, meaning that the sum of all human activities is a net removal of CO₂ from the atmosphere (95). On the other hand, a world in which all countries achieve an energy profile similar to that of the United States implies greater emissions than in RCP8.5 (88). Further, combustion of all remaining fossil fuels could lead to CO₂ concentrations on the order of 2000 ppm, with concentrations remaining over 1500 ppm for 1000 years (Fig. 3) (91).

Despite important uncertainties about the magnitude of future global warming, several sources of inertia make some future climate change a virtual certainty. Ocean thermal inertia causes global temperature to increase even after atmospheric CO₂ concentrations have stabilized (27, 35) and regional climate to change even after emissions have ceased and global temperature has stabilized (96). Carbon-cycle inertia and ocean thermal inertia cause global temperature to remain elevated long after emissions have stopped, even as CO₂ concentrations in the atmosphere decrease (34–36). If climate changes cause widespread forest loss and/or thawing of permafrost, substantial carbon input to the atmosphere could continue even after anthropogenic CO₂ emissions have ceased (97–99).

In addition to these physical, biogeochemical, and ecological sources of inertia, the human dimension of the climate system creates inertia that is likely to prolong and increase the level of global warming. The existing fossil-fuel-based economy creates inertia toward further CO₂ emissions. The life cycle of existing infrastructure and the knowledge base for generating wealth from fossil energy resources together imply that CO₂ emissions will continue for a minimum of another half-century (90). Human dynamics also create further inertia (92, 93). Increasing global population increases the global demand for energy, which in the current fossil-fuel-based energy system implies increasing global CO₂ emissions, even without economic development (88). However, demand for energy-enabled improvement in human well-being creates additional inertia (88), particularly given that 1.3 billion people currently lack reliable access to electricity, and 2.6 billion people rely on biomass for cooking (100). Last, the political process provides further inertia, both because emissions continue as political negotiations take place and because mitigation proposals are built around gradual emissions reductions that guarantee further emissions even if such proposals are eventually adopted (28, 101, 102).

Although not literally “committed,” these forms of inertia linked to human actions increase the likelihood that terrestrial ecosystems will face GHG concentrations that have rarely been encountered since the deep past. Ice core data confirm that atmospheric CO₂ concentrations have not been as high as at present for at least 800,000 years (Fig. 3) (103). Geochemical models and most proxy data also indicate CO₂ concentrations below 600 ppm—and, except for a small fraction of the record, below present levels—over the past 22 million years (Fig. 3) (104, 105). The trajectories of human population, energy demand, economic development, and climate policy therefore create the very real possibility that over the coming century, atmospheric CO₂ concentrations will be the highest of the past 22 million years (Fig. 3), with the trajectory of other GHGs further enhancing the total radiative forcing (30).

The Velocity of Climate Change

The rate of change in GHG concentrations and climate during the Anthropocene has been—and has the potential to continue to be—exceedingly rapid relative to past changes (Fig. 3 and fig. S1) (106–112). For example, although the global cooling that occurred between the early Eocene and the Eocene-Oligocene glaciation of Antarctica (52 to 34 million years ago) was greater than the 21st-century warming projected for RCP8.5, the Eocene cooling occurred over ~18 million years, making the rate of change many orders of magnitude slower than those of the RCPs

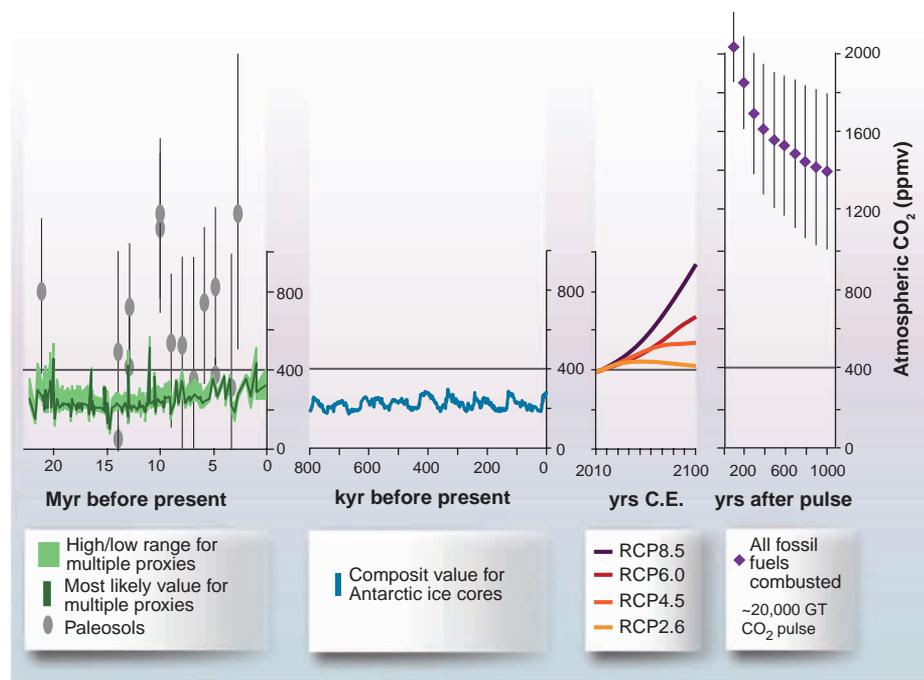


Fig. 3. Past and potential future atmospheric CO₂ concentrations. (Left) The high-low range of CO₂ over the past 22 million years from phytoplankton/forams, stomatal indices/ratios, and marine boron (105). (Middle left) CO₂ from Antarctic ice cores (103). (Middle right) CO₂ concentrations for different RCPs (30). (Right) The high-low range of CO₂ concentrations for the 1000-year time horizon after all fossil fuels are combusted (91). Further details are provided in the supplementary materials.



(fig. S1) (33, 112). Likewise, the Paleocene-Eocene Thermal Maximum (PETM) encompassed warming of at least 5°C in <10,000 years (113), a rate of change up to 100-fold slower than that projected for RCP8.5 and 10-fold slower than that projected for RCP2.6. Records from high-resolution ice cores indicate that regional climates can reorganize quickly, especially during glacial/interglacial transitions (114), but global rates of change during events such as the last glacial termination and the late-glacial/early-Holocene warming were all well below the minimum rate for the RCPs (fig. S1). Further, the rates of global change during the Medieval Climate Anomaly (MCA), Little Ice Age (LIA), and early Holocene were all smaller than the observed rates from 1880 to 2005 and than for the committed warming calculated to occur over the 21st century if atmospheric concentrations were capped at year-2000 levels (fig. S1).

The potentially unprecedented rate of global warming over the next century may present challenges for many terrestrial species as favorable climatic conditions shift rapidly across the landscape. Despite the fact that the tropics have exhibited the smallest absolute magnitude of warming (Fig. 1), the low background variability of annual and seasonal temperatures is causing temperature change to emerge most quickly from the background variability over the tropics (77, 115). In future decades, low-latitude warming (65, 77, 116) will likely expose many organisms in regions of high biodiversity and endemism to novel climate conditions, including frequent occurrence of unprecedented heat (Fig. 2) (116).

Another measure of potential climate stress is the velocity of climate change (8, 37), or the distance per unit of time that species need to move to keep conditions within the current local envelope (Fig. 4) (7, 8, 106, 108–110, 116–120). Different measures of velocity tend to emphasize either local topographic effects or large-scale climate patterns. Methods that understate the role of topography (Fig. 4) can miss the potential for the creation of climate refugia that could allow species to persist in the current range despite changes in large-scale climate conditions (15). Conversely, methods that underrepresent large-scale climate patterns ignore the critical fact that substantial changes can effectively push many species off the tops of mountains (121, 122) or the poleward edges of continents (Fig. 4). Moreover, biotic factors (8) such as evolutionary adaptation, dispersal ability, habitat suitability, and ecological interactions need also to be considered.

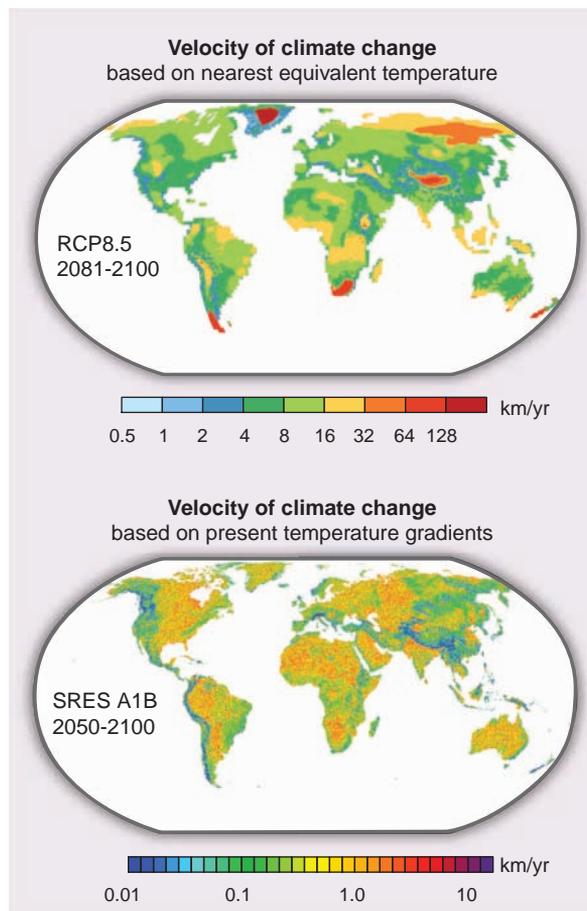


Fig. 4. The velocity of climate change. (Top) The climate change velocity in the CMIP5 RCP8.5 ensemble, calculated by identifying the closest location (to each grid point) with a future annual temperature that is similar to the baseline annual temperature. (Bottom) The climate change velocity [from (117)], calculated by using the present temperature gradient at each location and the trend in temperature projected by the CMIP3 ensemble in the SRES A1B scenario. The two panels use different color scales. Further details are provided in the supplementary materials.

The velocity of climate change may present daunting challenges for terrestrial organisms (7, 8, 69, 118, 123–129). Much of the world could experience climate change velocities greater than 1 km/year over the 21st century, and in some locations, the velocities could be much higher (Fig. 4) (8, 119). A rapidly increasing body of work (8, 11, 120, 129) has evaluated the dispersal potential of individual species in the context of expected velocities of climate change. Many species have the potential to keep pace with the shifting climate (8, 11, 120), but ability may or may not predict success. In some cases, the constraint may be no-analog climates, in which altered relationships between temperature and precipitation or novel patterns of extremes greatly restrict suitable habitat (14). In other cases, the limiting (or enhancing) factors may be the alteration of important biotic in-

teractions, the ability of existing species to hold onto habitat, or the presence of invasives that can quickly colonize and dominate available sites (11, 130). And in many locations, the constraint will be habitat fragmentation or degradation resulting from land use or air or water pollution (8, 131).

Conclusions

Terrestrial ecosystems have experienced widespread changes in climate over the past century. It is highly likely that those changes will intensify in the coming decades, unfolding at a rate that is at least an order of magnitude—and potentially several orders of magnitude—more rapid than the changes to which terrestrial ecosystems have been exposed during the past 65 million years. In responding to those rapid changes in climate, organisms will encounter a highly fragmented landscape that is dominated by a broad range of human influences. The combination of high climate-change velocity and multi-dimensional human fragmentation will present terrestrial ecosystems with an environment that is unprecedented in recent evolutionary history.

However, the ultimate velocity of climate change is not yet determined. Although many Earth system feedbacks are uncertain, the greatest sources of uncertainty—and greatest opportunities for modifying the trajectory of change—lie in the human dimension. As a result, the rate and magnitude of climate change ultimately experienced by terrestrial ecosystems will be mostly determined by the human decisions, innovations, and economic developments that will determine the pathway of GHG emissions.

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Supplementary Material for
Changes in Ecologically Critical Terrestrial Climate Conditions

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Materials and Methods

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1. Materials and Methods

1.1. Observed and projected changes in mean annual temperature and precipitation

We calculate the observed change in mean annual temperature and precipitation between the baseline period (1986-2005) and the mid-20th-century (1956-1975) using the CRU TS3.10.01 gridded station-based temperature and precipitation dataset (132). The CRU observations are available for land areas only. In Figure 1, we show differences between the baseline and mid-20th-century periods (1986-2005 minus 1956-1975). Areas where the calculation of percentage change in precipitation would require dividing by zero are masked.

We also use the CMIP5 global climate model ensemble (29) to calculate the change in annual temperature and precipitation between the baseline period (1986-2005) and the mid- (2046-2065) and late-21st-century (2081-2100) periods of the RCP8.5 forcing pathway (28, 30). We use all of the archived historical and RCP8.5 realizations from each of 27 global climate models that have archived temperature and precipitation fields from the RCP8.5 experiment (Table S1). The model realizations are aggregated as described in Diffenbaugh and Giorgi (65). Following (38, 65-66, 77, and references

therein), we interpolate each realization of each model to a common 1-degree geographical grid prior to performing the calculations.

In Figure 1, we show the multi-model mean difference between the baseline and future periods (future minus baseline). This presentation does not indicate significant differences from background variability, nor does it reflect many other potentially important sources of uncertainty, including level of emissions, Earth system feedbacks, and model structure (27). Approaches to indicating significant differences from background variability include (i) screening based on formal statistical significance testing of the baseline and future populations (27, 71), and (ii) quantifying the fraction of ensemble spread contributed by intra-model variations (84-85). Approaches to indicating uncertainty due to differences in model structure include (i) screening for agreement in the sign of change (22), (ii) screening for ensemble-mean changes that exceed the spread between the individual model changes (27, 66), (iii) plotting different quantiles of the ensemble values (77), and (iv) quantifying the fraction of ensemble spread contributed by inter-model differences (85). Approaches to indicating uncertainty in the level of emissions include quantifying the fraction of ensemble spread contributed by different emissions scenarios (85), while approaches to indicating uncertainty from Earth system feedbacks include comparing projections of the same models with and without different Earth system components (such as the carbon cycle) (27).

In Figure 1, the values at the left and right extremes of the color bars give the minimum and maximum values (respectively) that occur across all of the periods. The minimum temperature, minimum precipitation, and maximum precipitation extreme changes are all in the CRU (observed) dataset.

1.2. Observed and projected changes in the occurrence of extreme seasonal temperature, precipitation, and snow accumulation

We show the occurrence of extreme seasons published in Diffenbaugh and Giorgi (65), Diffenbaugh et al. (66), and Diffenbaugh and Scherer (77). The upper left panel of Figure 2 shows how often the 1986-2005 maximum seasonal temperature occurs in the 2046-2065 period of RCP8.5 [from Diffenbaugh and Giorgi (65)]. The lower left panel of Figure 2 shows how often the 1986-2005 minimum seasonal precipitation occurs in the 2080-2099 period of RCP8.5 [from Diffenbaugh and Giorgi (65)]. The lower right panel of Figure 2 shows how often the 1976-2005 minimum March snow water equivalent occurs in the 2070-2099 period of RCP8.5, with black stippling indicating areas where the multi-model mean exceeds 1.0 standard deviations of the multi-model spread, and with white stippling indicating areas where the multi-model mean exceeds 2.0 standard deviations of the multi-model spread [from Diffenbaugh et al. (66)]. The upper right panel of Figure 2 shows the time series of the fraction of land grid points in northern South America (25S-3N, 82-33W) with JJA surface air temperatures exceeding the respective 1952-1969 maxima [from Diffenbaugh and Scherer (77)]. The grey points denote this fraction for each CMIP3 realization. The black curve shows the mean across all realizations. The red curve shows the 10-year running mean of the mean across all realizations. The blue curves show the 10-year running mean of a one-standard-deviation range across the mean of all realizations. The light purple curve shows the observational timeseries. The dark purple curve shows the 10-year running mean of the observational timeseries. The trend in the observational timeseries (% of region per year) is shown in

the upper left of the panel, with the * indicating that the trend is statistically significant. The mean of the trends in the CMIP3 realizations is shown in plain text in the upper right of the panel, with the number of realizations (out of 52) that exhibit a statistically significant trend shown in bold.

1.3. Past and potential future atmospheric carbon dioxide concentrations

We show timeseries of atmospheric carbon dioxide (CO₂) concentrations from geologic proxies, ice core measurements, and illustrative potential future pathways reported in the published, peer-reviewed literature. In Figure 3, the left panel shows reconstructed CO₂ concentrations reported by Royer (105) for the past 22 million years. The light gray symbols show the values for paleosols, with the circle showing the most likely value and the black bar showing the maximum/minimum range. The dark green curve shows the timeseries of the most likely values for the other proxies reported by Royer (105), while the light green field shows the timeseries of the maximum/minimum range. The left-center panel shows the timeseries of composite CO₂ concentrations from Antarctic ice cores reported by Lüthi et al. (103) for the past 800 kyr. The right-center panel shows the RCP concentrations for the 21st century [from van Vuuren et al. (30)]. The right panel shows the range of atmospheric CO₂ concentrations for the first 1,000 years after a pulse of 5,000 PgC is combusted [reported in Archer et al. (91)]. The black bar shows the maximum/minimum range across the models assessed by Archer et al. (91), while the purple diamond shows the mean of the maximum and minimum values.

1.4. Rate and magnitude of global-scale temperature change during the geologic past and illustrative potential futures

We show rates and magnitudes of global-scale temperature change from paleoclimate proxies, instrumental observations, and climate model simulations reported in the published, peer-reviewed literature. The RCP values are from the global temperature ranges published in Rogelj et al. (33). “Infrastruct.” is the range of warming resulting from emissions from existing infrastructure reported in Davis et al. (90). “Year-2000” shows the committed warming associated with stabilizing atmospheric concentrations at the year-2000 values, calculated from the multi-model range reported in Figure 10.4 of Meehl et al. (27). “1880-2005” and “1980-2005” show the observed ranges of rate and magnitude of warming over the 1880-2005 and 1980-2005 periods of the instrumental record, calculated from the observed global temperature timeseries reported in Figure 3.1 of Trenberth et al. (23). “52-34 Ma” shows the long-term cooling between 52 million years ago and 34 million years ago [calculated from Zachos et al. (112)]. “Oi-1” shows the glaciation near the Eocene-Oligocene boundary [calculated from Zachos et al. (112)]. “PETM” shows the Paleocene-Eocene Thermal Maximum, based on the characterization of Zachos et al. that “global temperature increased by more than 5 °C in less than 10,000 years” (113). “Last Degl.” shows the difference between the Last Glacial Maximum and present, using the 95% confidence interval of 3.1-4.7 °C cooling from Annan and Hargreaves (133) and a Last Glacial Maximum date of 21,000 years before present. “End Glacial” shows the warming at the end of the last glacial and the early Holocene, calculated from Shakun et al. (134). “Early Hol.” shows the warming during the early Holocene, “MCA” shows the warming during the Medieval Climate

Anomaly, and “LIA” shows the cooling during the Little Ice Age, with each calculated from Marcott et al. (135).

1.5. The velocity of climate change

We calculate the velocity of climate change (km/yr) using the mean annual temperature in the CMIP5 ensemble (29), and correcting for baseline-period noise [e.g., (77, 110, 116)]. For a given grid point, we first calculate the difference between that grid point’s multi-model mean annual temperature in the baseline period and all other grid points’ multi-model mean annual temperature in the 2081-2100 period of RCP8.5. We then identify all grid points for which the absolute value of that difference is less than the multi-model mean of the baseline-period noise of the given grid point (calculated as the standard deviation of the 20-year running mean of the 1967-2005 time series). We then select the closest of those identified grid points, yielding the minimum distance needed to maintain the current annual temperature regime in the future climate. We then divide that minimum distance by 1 century, yielding the velocity of climate change for that given grid point.

In Figure 4, the upper panel shows our CMIP5-based calculation of the velocity of climate change. The bottom panel shows the velocity of climate change from Loarie et al. (117), who used the present temperature gradient at each location ($^{\circ}\text{C}/\text{km}$) and the rate of warming at each location in the 2050–2100 period of the Special Report on Emissions Scenarios (SRES) A1B emissions scenario ($^{\circ}\text{C}/\text{yr}$) to calculate the velocity (km/yr).

Table S1. CMIP5 models used to calculate the annual mean temperature and precipitation in the RCP8.5 forcing pathway.

Model Name
ACCESS1-0
ACCESS1-3
bcc-csm1-1
BNU-ESM
CanESM2
CCSM4
CMCC-CM
CNRM-CM5
CSIRO-Mk3-6-0
FGOALS-g2
FGOALS-s2
FIO-ESM
GFDL-ESM2G
GFDL-ESM2M
GISS-E2-R
HadGEM2-AO
HadGEM2-CC
HadGEM2-ES
inmcm4
IPSL-CM5A-LR
IPSL-CM5B-LR
MIROC5
MIROC-ESM-CHEM
MIROC-ESM
MPI-ESM-LR
MRI-CGCM3
NorESM1-M

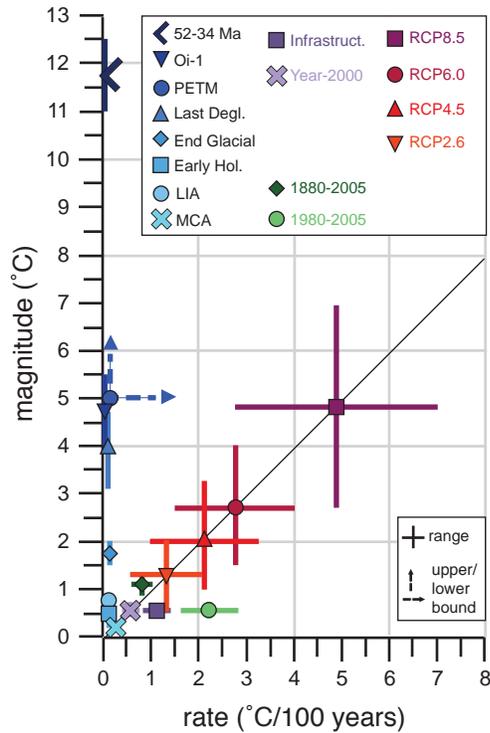


Fig. S1. Rate and magnitude of global-scale temperature change during the geologic past and illustrative potential futures. Global temperature ranges are shown based on the uncertainty ranges given in the literature. RCP values are from global temperature ranges in Rogelj et al. (33). “Infrastructure” and “Year-2000” commitments are calculated from Davis et al. (90) and Meehl et al. (27), respectively. “1880-2005” and “1980-2005” are calculated from the observed global temperature timeseries reported in Trenberth et al. (23). Paleoclimate events are calculated from the values provided in Zachos et al. (112-113), Annan and Hargreaves (133), Shakun et al. (134), and Marcott et al. (135). Further details are provided in the supplemental materials.

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REVIEW

Marine Ecosystem Responses to Cenozoic Global Change

R. D. Norris,^{1*} S. Kirtland Turner,¹ P. M. Hull,² A. Ridgwell³

The future impacts of anthropogenic global change on marine ecosystems are highly uncertain, but insights can be gained from past intervals of high atmospheric carbon dioxide partial pressure. The long-term geological record reveals an early Cenozoic warm climate that supported smaller polar ecosystems, few coral-algal reefs, expanded shallow-water platforms, longer food chains with less energy for top predators, and a less oxygenated ocean than today. The closest analogs for our likely future are climate transients, 10,000 to 200,000 years in duration, that occurred during the long early Cenozoic interval of elevated warmth. Although the future ocean will begin to resemble the past greenhouse world, it will retain elements of the present “icehouse” world long into the future. Changing temperatures and ocean acidification, together with rising sea level and shifts in ocean productivity, will keep marine ecosystems in a state of continuous change for 100,000 years.

Marine ecosystems are already changing in response to the multifarious impacts of humanity on the living Earth system (1, 2), but these impacts are merely a prelude to what may occur over the next few millennia (3–9). If we are to have confidence in projecting how marine ecosystems will respond in the future, we need a mechanistic understanding of Earth system interactions over the full 100,000-year time scale of the removal of excess CO₂ from the atmosphere (10). It is for this reason that the marine fossil record holds the key to understanding our future oceans (Fig. 1). Here, we review the marine Cenozoic record [0 to 66 million years ago (Ma)], contrast it with scenarios for future oceanic environmental change, and assess the implications for the response of ecosystems.

In discussions of the geologic record of global change, it is important to distinguish between

mean and transient states. Mean climate states consist of the web of abiotic and biotic interactions that develop over tens of thousands to millions of years and incorporate slowly evolving parts of Earth's climate, ocean circulation, and tectonics. Transient states, in comparison, are relatively short intervals of abrupt (century- to millennium-scale) climate change, whose dynamics are contingent on the leads and lags in interactions among life, biogeochemical cycles, ice growth and decay, and other aspects of Earth system dynamics. Ecosystems exhibit a range in response rates: Animal migration pathways and ocean productivity may respond rapidly to climate forcing, whereas a change in sea level may reset growth of a marsh (11) or sandy bottoms on a continental shelf (12) for thousands of years before these ecosystems reach a new dynamic equilibrium. Thus, both mean and transient dynamics are important for understanding past and future marine ecosystems (13).

Past Mean States: The Cenozoic

The evolution of marine ecosystems through the Cenozoic can be loosely divided into those of the “greenhouse” world (~34 to 66 Ma) and those

of the modern “icehouse” world (0 to 34 Ma) (Fig. 1). We explore what these alternative mean states were like in terms of physical conditions and ecosystem structure and function.

Greenhouse World Physical Conditions

Multiple lines of proxy evidence suggest that atmospheric partial pressure of CO₂ (*p*CO₂) reached concentrations above 800 parts per million by volume (ppmv) between 34 and 50 Ma (14) (Fig. 2). Tropical sea surface temperatures (SSTs) reached as high as 30° to 34°C between 45 and 55 Ma (Fig. 2). The poles were unusually warm, with above-freezing winter polar temperatures and no large polar ice sheets (15, 16). Because most deep water is formed by the sinking of polar surface water, the deep ocean was considerably warmer than now, with temperatures of 8° to 12°C during the Early Eocene (~50 Ma) versus 1° to 3°C in the modern ocean (15). The lack of water storage in large polar ice sheets caused sea level to be ~50 m higher than the modern ocean, creating extensive shallow-water platforms (15, 17).

In the warm Early Eocene (~50 Ma), tectonic connections between Antarctica and both Australia and South America allowed warm subtropical waters to extend much closer to the Antarctic coastline, helping to prevent the formation of an extensive Antarctic ice cap (16) and limiting the extent of ocean mixing and nutrient delivery to plankton communities in the Southern Ocean (18). Tectonic barriers and a strong poleward storm track maintained the Arctic Ocean as a marine anoxic “lake” with a brackish surface-water lens over a poorly ventilated marine water column (19). Indeed, the Arctic surface ocean was occasionally dominated by the freshwater fern *Azolla*, indicating substantial freshwater runoff (20).

Greenhouse World Ecosystems

The warm oceans of the early Paleogene likely supported unusual pelagic ecosystems from a modern perspective. The warm Eocene saw oligotrophic open-ocean ecosystems that extended to the mid- and high latitudes and productive equatorial zones that extended into what is now the

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warm subtropics (17). In the modern ocean, most primary productivity in warm, low-latitude gyres is generated by small phytoplankton with highly

efficient recycling of organic matter and nutrients (21). Such picophytoplankton-dominated ecosystems typically support long food chains

where the loss of energy between trophic levels limits the overall size of top predator populations (5, 22). Although the radiations of many

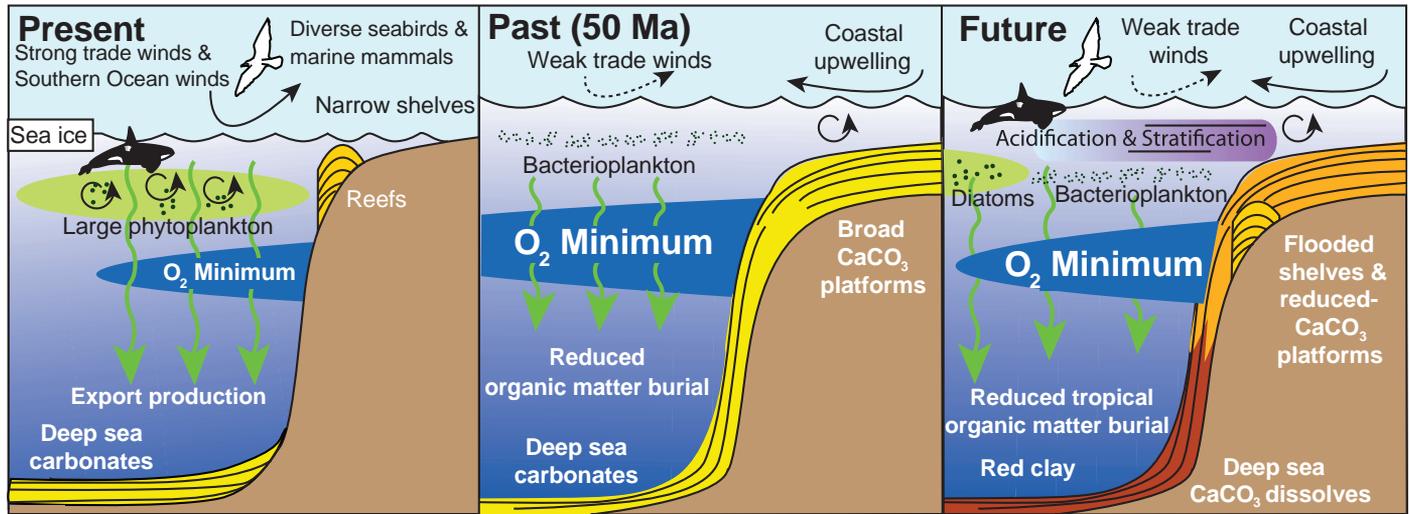


Fig. 1. Comparison of present, past, and future ocean ecosystem states. In the geologic past (middle panel), a warmer, less oxygenated ocean supported longer food chains based in phytoplankton smaller than present-day phytoplankton (left panel). The relatively low energy transfer between trophic levels in the past made it hard to support diverse and abundant top predators dominated by marine mammals and seabirds, and also reduced deep-sea organic matter burial. Equilibration of weathering with high atmospheric pCO_2 allowed carbonates to accumulate in parts of the deep sea. Reef construction was limited by high temperatures and coastal runoff even as high

sea level created wide, shallow coastal oceans. In the future (right panel), warming will eventually reproduce many features of the past warm world but will also add transient impacts such as acidification and stratification of the surface ocean. Acidification will eventually be buffered by dissolving carbonates in the deep ocean, which create carbonate-poor “red clay.” Stratification and the disappearance of multiyear sea ice will gradually eliminate parts of the polar ecosystems that have evolved in the past 34 million years and will restrict the abundance of short-food chain food webs that support marine vertebrates in the polar seas.

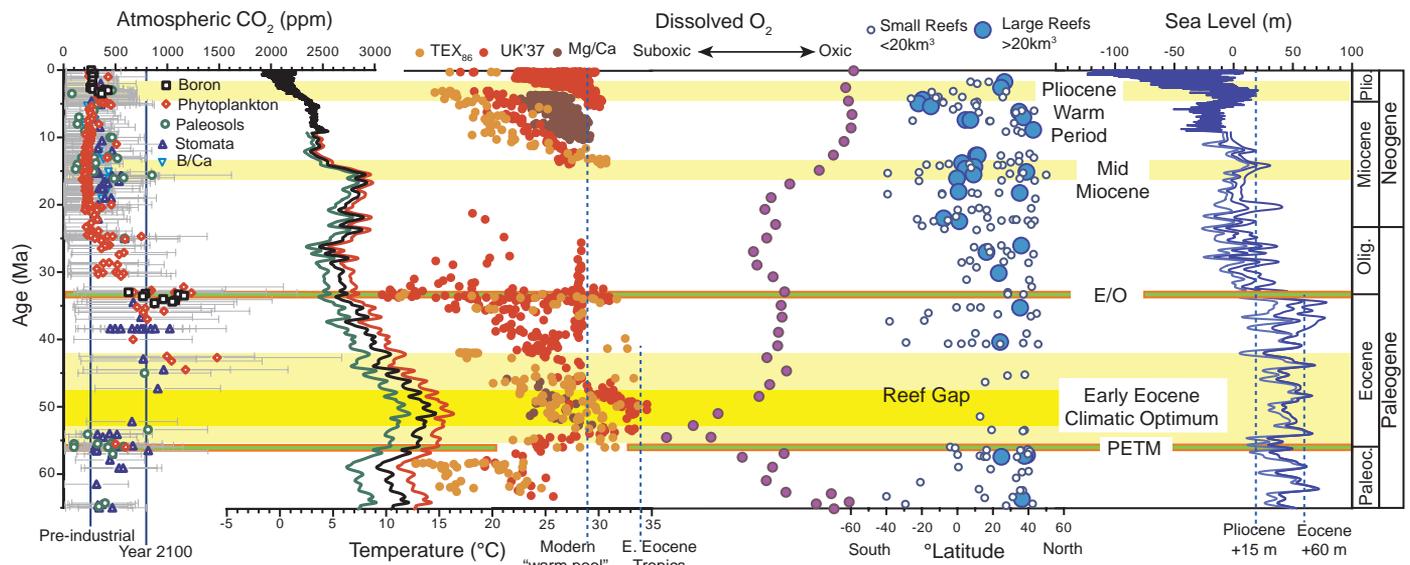


Fig. 2. Cenozoic record of major ecosystem drivers and responses. From left to right: Proxy evidence for atmospheric pCO_2 (14); vertical lines show the preindustrial pCO_2 (280 ppm) and estimated pCO_2 for year 2100 under a business-as-usual emissions scenario. Deep ocean temperature (15) estimated from oxygen isotope and Mg/Ca proxy evidence. Black line is long-term average for benthic foraminifera, red line is temperature adjusted for pH, and green line is temperature adjusted for seawater $\delta^{18}O$ effects. Compilation of surface ocean temperature estimates from multiple organic matter and Mg/Ca proxies (as indicated by different colors) (37, 90–98); data are plotted with their published

assumptions and age models. (Although the age models may differ slightly, these differences are not apparent at this resolution.) Dissolved O_2 is estimated from the Benthic Foraminifer Oxygen Index in a global compilation (99). Reef volume and temporal distribution (31); reefs with estimated volumes greater than 20 km^3 are plotted in large solid circles, smaller reefs as open circles. Sea level is estimated from combined benthic foraminifer $\delta^{18}O$, Mg/Ca, and the New Jersey sea-level record: long-term average (middle line) and uncertainty (maximum, minimum lines). Dotted vertical lines show the estimated average high stands for the Pliocene and Eocene.

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pelagic predators (including the whales, seals, penguins, and tunas) began in the greenhouse world of the late Cretaceous and early Paleogene, their modern forms and greatest diversity were achieved later, as large diatoms emerged as important primary producers and food chains became shorter and more diverse in the icehouse world (Fig. 3).

Multiple lines of evidence suggest that early Paleogene (45 to 65 Ma) ecosystems differed from the modern with respect to the organic carbon cycle (23, 24). The greenhouse ocean was about as productive as today, but more efficient recycling of organic carbon led to low organic carbon burial (23, 25). There were also major radiations of midwater fish, such as lanternfish and anglerfish (26), and diversifications of planktonic foraminifer communities typical of low-oxygen environments between 45 and 55 Ma (27, 28) (Figs. 2 and 3).

Coral-algal reef systems existed throughout the low- to mid-latitude Tethys Seaway from ~58 to 66 Ma (Fig. 2) (29). During the very warm, high- $p\text{CO}_2$ interval between ~42 and 57 Ma, coral-dominated large reef tracts were replaced by foraminiferal-algal banks and shoals (30, 31). This “reef gap” was present throughout Tethys, Southeast Asia, Pacific atolls, and the Caribbean (29, 31–33). The timing of the Tethyan reef gap suggests that the loss of architectural reefs was related to some combination of unusual warmth of the tropics and hydrologic changes in sedimentation and freshwater input (34, 35). Notably,

many modern groups of reef fishes evolved before or during this time (26, 36), which suggests that the changing biogeography of metazoan reefs and extensively flooded continental shelves may have contributed to their evolution.

Icehouse World Physical Conditions

Atmospheric $p\text{CO}_2$, which had been ~700 to 1200 ppmv during the late Eocene, fell to 400 to 600 ppmv across the Eocene-Oligocene boundary (34 Ma) (37). The decline in greenhouse gas forcing caused tropical SSTs to fall to values within a few degrees of those in the modern “warm pool” western Pacific or western Atlantic (~29° to 31°C) by 45 Ma (37) (Fig. 2). At high latitudes, deep ocean temperatures declined to 4° to 7°C between 15 and 34 Ma, with further polar cooling over the past 5 million years (15).

Polar cooling and Antarctic ice growth between ~30 and 34 Ma occurred as CO_2 levels declined (38) and were accompanied by the tectonic separation of Antarctica from Australia and eventually South America (17). Establishment of the Antarctic Circumpolar Current increased the pole-to-equator temperature gradient, increased the upwelling of nutrients and biogenic silica production in the Southern Ocean, and initiated modern polar ecosystems (39, 40). The growth of polar ice at ~34 Ma produced a sea-level fall of ~50 m, and the later growth of Northern Hemisphere ice sheets at 2.5 Ma initiated a cycle of sea-level fluctuations of up to 120 m (41, 42). In the Arctic, the ecosystem evolved from a marine anoxic “lake”

to a basin with perennial sea ice cover by at least 14 Ma (43).

Icehouse World Ecosystems

By 34 Ma, an ecosystem shift occurred in the high southern latitudes (40) as better wind-driven mixing in the Southern Ocean supported diatom-dominated food chains. The resulting short food chains fueled a major diversification of modern whales (39, 44), seals (45), seabirds (46, 47), and pelagic fish (48) (Fig. 3). The onset of Southern Ocean cooling is closely timed with the appearance of fish- and squid-eating “toothed” mysticetes at ~23 to 28 Ma and the radiation of large bulk-feeding baleen whales beginning at ~28 Ma (49). It is hypothesized that tropical and upwelling diatom productivity—initiated by nutrient leakage out of the high latitudes—spurred the development of long-distance migration by the great whales in the past 5 to 10 million years (39). This interval also coincides with radiations of delphinids (50), penguins (46), and pelagic tunas (48) (Fig. 3). The diversification of Arctic and Antarctic seals also unfolded during the past 15 million years as polar climates intensified and sea ice habitats expanded (45).

Reefs expanded in low to mid-latitudes, particularly in the northern subtropical Mediterranean and western Pacific, by ~42 Ma (31). However, the major growth of large reefs mostly occurred from ~20 Ma to the present, with major expansions of reef tracts in the southwestern

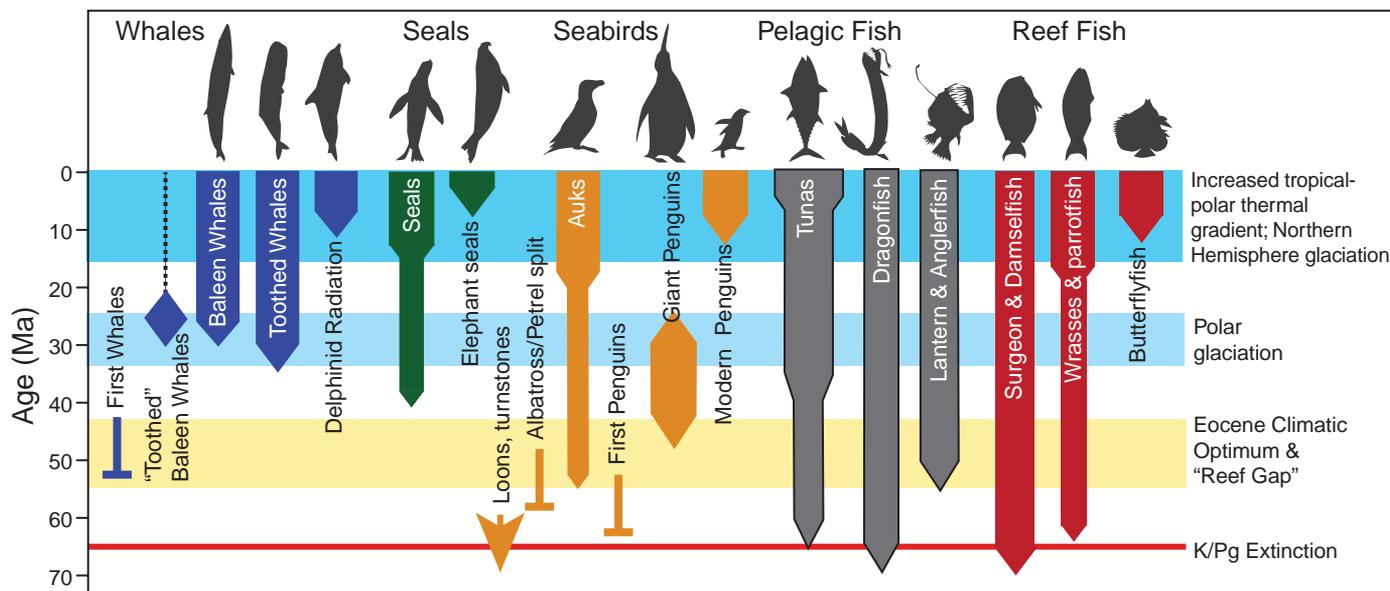


Fig. 3. Evolutionary events and diversification of selected marine vertebrate groups. Radiations of marine birds, tuna, mid-pelagic fish (e.g., dragonfish), and various groups of reef fish occur at or before the Cretaceous-Paleogene (K/Pg) mass extinction (65 Ma). The Eocene Climatic Optimum (45 to 55 Ma) is associated with the first whales (44), radiations of pelagic birds [albatrosses (100), auks (47), and penguins (46)], and diversification of midwater lanternfish and anglerfish (26).

With the onset of Antarctic glaciation (~34 Ma) and development of the Circum-Antarctic current, there is the major diversification of whales (49) and giant, fish- and squid-eating penguins (46). The differentiation of polar and tropical climate zones at ~8 to 15 Ma is associated with the extensive diversification of coastal and pelagic delphinids (50), Arctic and Antarctic seals (45), auks (47), modern penguins (46), pelagic tuna (48), and reef fishes (52, 53).

Pacific and the Mediterranean (31, 51). Several large groups of reef-associated fish, such as wrasses (52), butterflyfish (53), and damselfish (51), experienced radiations between 15 and

20 Ma (Fig. 3). These fishes include reef obligates, such as clades associated with coral feeding, that diversified along with the geographic expansion of fast-growing branching corals (53).

Sea-level variations in the past 34 million years had major impacts on shaping shallow marine ecosystems. The break in slope between the gentle shelf and the relatively steep slope

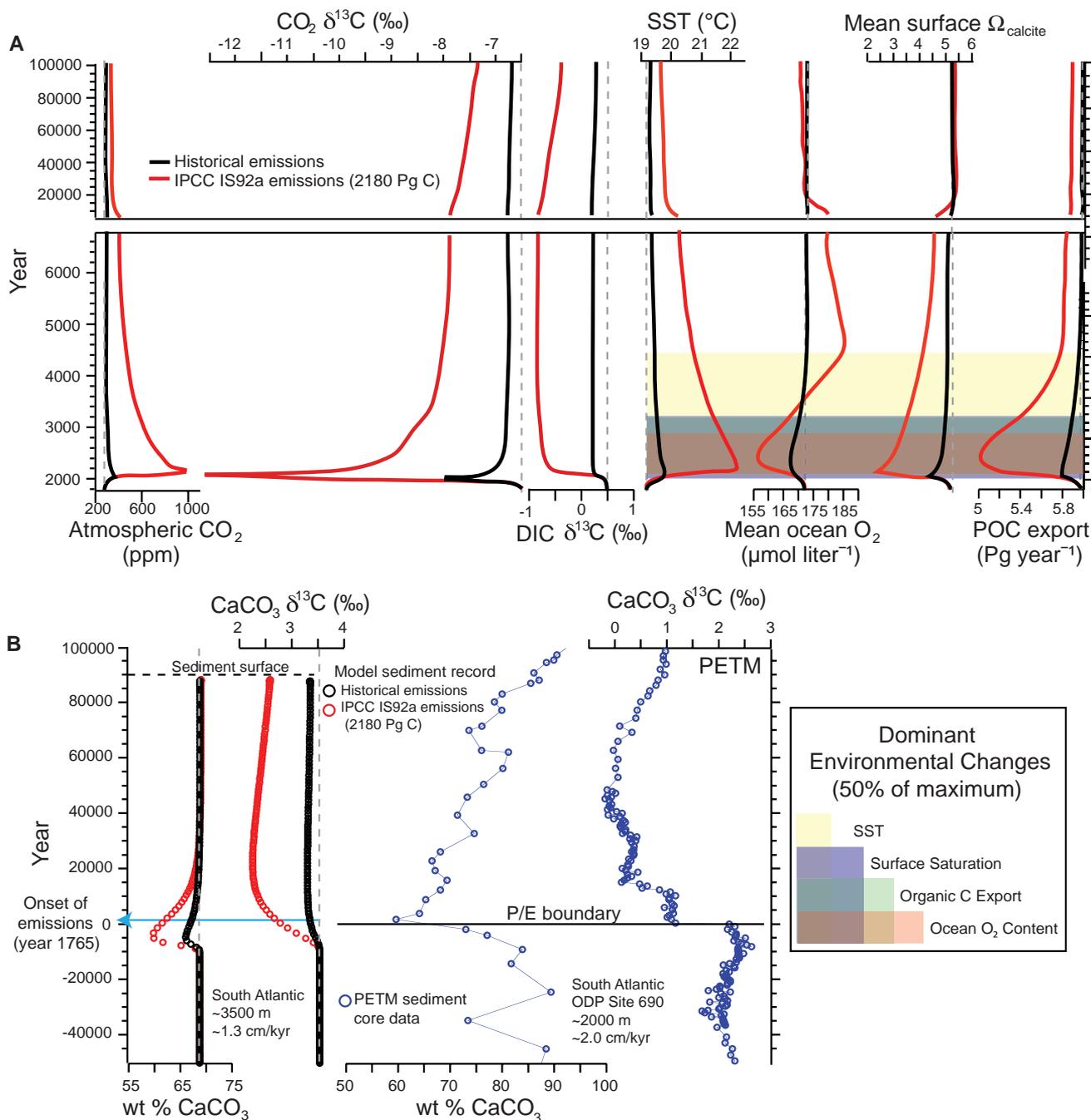


Fig. 4. Future Earth model. (A) 100,000-year simulations of historical anthropogenic CO₂ emissions (black lines) and the IPCC IS92a emissions (red lines). From left to right: the evolution of atmospheric CO₂, the δ¹³C of CO₂, the δ¹³C of dissolved inorganic carbon (DIC), SST, mean ocean O₂, surface ocean carbonate saturation with respect to calcite, and particulate organic matter (POC) export (modeled from a simple relationship with phosphate inventories). Note that some records such as the δ¹³C of DIC do not recover fully in even 100,000 years. Color bars highlight the interval in which each environmental variable (SST, mean ocean O₂, calcite saturation state, and organic C export) shows at least 50% of

the total change. (B) Modeled sedimentary expressions of the scenarios shown in (A) from a model site with a sedimentation rate of 1.3 cm per 1000 years (typical of the deep sea). Profiles show the weight percent CaCO₃ in sediments (left) and the δ¹³C of sedimentary carbonates (right). Although both scenarios were initiated in year 1765 (to simulate the start of the Industrial Revolution), dissolution of sea-floor carbonates and mixing by burrowers shifts the apparent start date substantially earlier than this. The PETM (blue lines, right) has a CaCO₃ minimum (101) and a δ¹³C minimum (102) comparable in duration, but larger in magnitude, than the simulated future.



occurs at ~100 m on most continental margins. In the later Pleistocene, glacially driven sea-level falls produced major decreases in shallow marine habitat area, fragmented formerly contiguous ranges of coastal species, and disrupted barrier reef growth (54–56). Sea level rose during glacial terminations at a pace of ~1 m per 100 years (57), a pace readily matched by the dispersal of benthic marine invertebrates and algae. However, Pleistocene sea-level rise was fast enough to trap sand in newly formed estuaries and create transient ecosystems such as marshes, sandy beaches, and sand-covered shelves over time scales of several thousand years (11, 55).

Lessons from Cenozoic Mean States

Past warm climates had warmer-than-modern tropics, extensively flooded continental margins, few architectural reefs, more expansive midwater suboxic zones, and more complete recycling of organic matter than now. Tropical oceans were likely as productive as today, but the productive waters expanded into the subtropics and supported long food chains based in small phytoplankton. Today, the inefficiency of energy transfer in picophytoplankton-dominated ecosystems limits the overall size of top predator populations and probably did so in the past. Although some of these conditions may recur in the future, tectonic boundary conditions are likely to prevent polar ecosystems from completely reverting to their past greenhouse world configurations in the near future. Hence, it seems unlikely that the Arctic “lake” will be reestablished or that wind-driven mixing will diminish enough in the Southern Ocean to destroy ecosystems founded on short, diatom-based food chains.

Past Transient Global Change Impacts: The Paleocene-Eocene Thermal Maximum

One of the best-known examples of a warm climate transient is the Paleocene-Eocene Thermal Maximum (PETM), a period of intense greenhouse gas–fueled global change 56 million years ago. The PETM is characterized by a 4° to 8°C increase in SSTs, ecosystem changes, and hydrologic changes that played out over ~200,000 years (58). Warm-loving plankton migrated poleward, and tropical to subtropical communities were replaced by distinctive “excursion” faunas and floras (35). Open-ocean plankton were dominated by species associated with low-productivity settings, whereas shallow shelf communities commonly became enriched in taxa indicative of productive coastal environments (59). Numerous in-

dicators suggest that toward the close of the PETM (100,000 years after it began), there was a widespread increase in ocean productivity (60, 61) and a transient rise in the carbonate saturation state above pre-PETM levels (62) due to intensified chemical weathering during the event (63).

The only major extinctions occurred among deep-sea benthic foraminifera (50% extinction) (35, 64). Surviving benthic foraminifera reduced their growth rate, increased calcification, and switched community dominance toward species accustomed to high food supplies and/or low-oxygen habitats (65). Deep-sea ostracodes also became dwarfed and shorter-lived, and many species vacated the deep sea into refugia for the duration of the PETM (35, 66). The preferential extinction of benthic foraminifera and temporary disappearance of ostracodes in the deep sea is attributed to a combination of a drop in export production associated with stratification in low and mid-latitudes, a marked drop in deep-sea dissolved oxygen concentrations related to transient ocean warming, and/or reduced carbonate saturation related to uptake of atmospheric CO₂ inventories (35, 64, 66, 67).

There are indications of a possible drop in carbonate saturation during the PETM, such as the common occurrence in a few species of malformed calcareous phytoplanktonoliths and planktic foraminifera (68). However, the evolution of reef ecosystems through the PETM argues against severe surface-ocean acidification. For instance, a Pacific atoll record does not record a distinct sedimentary change or dissolution event (69). In the Tethys Seaway, large coral-algal reefs disappeared prior to the PETM, but coral knobs persisted into the early Eocene amid the dominant foraminiferal-algal banks and mounds (34, 35). Hence, if there was surface-ocean acidification during the PETM, its effects were modest and did not precipitate a major wave of extinction in the upper ocean.

The Geologic Record of the Future: Diagnosing Our Own Transient

How representative are transient events like the PETM for Earth’s near future? We compared the PETM record to a modeled future of the historical record of CO₂ emissions (Fig. 4A, black lines) and the Intergovernmental Panel on Climate Change (IPCC) IS92a emissions scenario (peak emissions rate of 28.9 Pg C year⁻¹ in 2100; total release of 2180 Pg C) (Fig. 4A, red lines). The latter represents a conservative future, given the availability of nearly twice as much carbon in fossil fuels.

We used the Earth system model cGENIE, including representation of three-dimensional ocean circulation, simplified climate and sea ice feedbacks, and marine carbon cycling (including deep-sea sediments and weathering feedbacks) (70, 71). In both long-term (10,000 years) (10) and historical perturbation (72) experiments, cGENIE responds to CO₂ emissions in a manner consistent with higher-resolution ocean models. Experiments were run after a 75,000-year model spin-up, needed to fully equilibrate deep-sea surface sediment composition.

Under the IPCC IS92a emissions scenario, CO₂ peaks at ~1000 ppmv just after year 2100 (Fig. 4A). The emission of a large mass of fossil fuel carbon causes a ~6‰ drop in atmospheric δ¹³C and a ~1‰ drop in carbonate δ¹³C—an event less than half the size of the PETM anomaly (73). SSTs increase by 3°C, reaching a maximum just before year 2200, and remain elevated above preindustrial SSTs by almost 0.5°C for >100,000 years (Fig. 4A). Here again, the estimated PETM surface ocean temperature anomaly is larger, at 5° to 9°C (58, 73). In the future scenario, the CO₂ invasion of the surface ocean causes the mean calcite saturation state of the surface ocean (Ω) to drop to a minimum of 2 Ω just after year 2100,

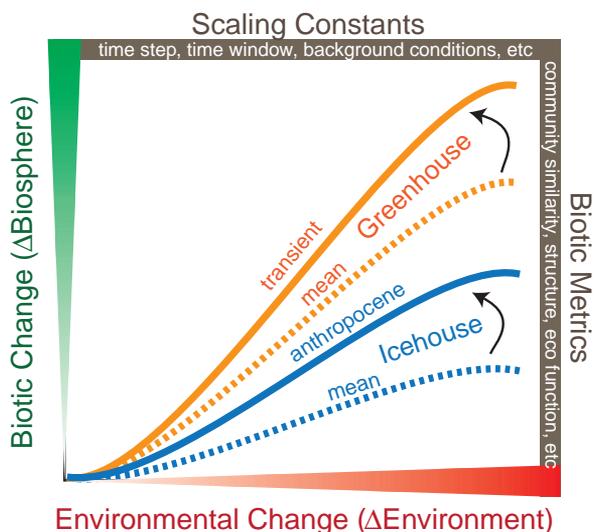


Fig. 5. Hypothetical biotic response to global change. Biotic sensitivity describes the response of ecosystems to a given amount of environmental change. It is currently unknown whether biotic sensitivity is constant in differing background conditions. For instance, here we illustrate the possibility that biotic sensitivity changes with climate state. This could occur if species exhibited broader environmental tolerances in icehouse climates, conferring greater biotic resilience across communities more generally. Modern global change is expected to change ecosystem structure in the direction of past greenhouse transient events. Additional research is needed to determine whether biotic sensitivity varies by taxa and ecosystem metrics (biotic metrics), sampling intervals, study durations, and background conditions (scaling constants). Our understanding of biotic sensitivity will determine our ability to predict future biotic changes over the next 50,000 to 100,000 years.

accompanied by a decrease in CaCO_3 export. The global average hides the extensive regions of the world ocean that will become undersaturated with respect to calcite and, in particular, aragonite (74)—with profound biological effects (75, 76), including the possible cessation of all coral reef growth (77). Eventually, a temporary buildup of weathering products leads to an overshoot in Ω beginning around year 13,500 that persists through the remaining 100,000 years—an effect also observed after the PETM (78, 79). Mean ocean oxygen concentration is modeled to drop to a minimum at year 2500, return to preindustrial levels a thousand years later, and then increase above modern values for ~12,000 years as a result of the resump-

tion of strong ocean overturning and decreased export of particulate organic carbon. Both a drop in O_2 and export production also occurred in the early stages of the PETM (35).

The modeled sedimentary expression of the future is broadly similar to the PETM (Fig. 4B). The decrease in carbonate $\delta^{13}\text{C}$ and weight percent CaCO_3 is greater for the PETM than for the modeled future, consistent with a greater mass of carbon injected during the PETM than in the conservative future emissions scenario of 2180 Pg C. A striking aspect of the modeled future record is that the onset of the $\delta^{13}\text{C}$ excursion does not appear notably more rapid than for the PETM. Both sediment mixing (bioturbation) and carbonate dissolution act to shift the apparent onset of a

transient event into geologically older material and reduce the apparent magnitude of peak excursions (80, 81).

Biotic Sensitivity and Ecosystem Feedbacks

Ecological and environmental records from past oceans provide guideposts constraining the likely direction of future environmental and ecological change. They do not, however, inform key issues such as the likelihood that ecosystems will change or how they may mitigate or amplify global change. These are all questions of biotic sensitivity and ecosystem feedbacks.

Biotic sensitivity describes the equilibrium response of the biosphere to a change in the environment (Fig. 5). There is tantalizing evidence that ecosystem responses scale with the size of transient warming events in the same way that surface temperature scales with $p\text{CO}_2$ concentrations [i.e., climate sensitivity (82)]. Specifically, Gibbs *et al.* (83) found that change in nanoplankton community structure (Σ_{CV}) scaled with the magnitude of environmental change (as measured by $\delta^{13}\text{C}$) during a succession of short-lived global change events between 53.5 and 56 Ma. This result suggests that “background” biotic sensitivity can predict responses to much larger perturbations. Additional studies of biotic sensitivity in deep time are urgently needed to test whether this type of scaling exists across taxa and different ecosystems or with changes in background conditions, time scale, or time step (Fig. 5).

Ecosystem feedbacks have the potential to mitigate or amplify the environmental and ecological effects of current greenhouse gas emissions. For instance, the greenhouse gas anomaly of the PETM is drawn down more quickly than would be expected by physical Earth system feedbacks alone (60, 84). Widespread evidence for a burst in biological productivity in the open marine environments (60, 61) and indirect evidence for increased terrestrial carbon stores during termination of the PETM (84) support the hypothesized importance of negative ecosystem feedbacks in driving rapid carbon sequestration. Species-specific responses to environmental perturbation—including growth rates (85), dwarfing (86), range shifts (87), or loss of photosymbionts (88)—can affect the structure and function of entire ecosystems. For instance, ecological interactions are hypothesized to have an important influence in setting the carbonate buffering capacity of the world’s ocean (70, 71) and in driving Cenozoic-long trends in the carbonate compensation depth (89), among many others. The geological record of transient events has the largely unexploited potential to constrain the type and importance of ecosystem feedbacks.

Lessons for the Future

The near future is projected to be a cross between the present climate system and the Eocene-like

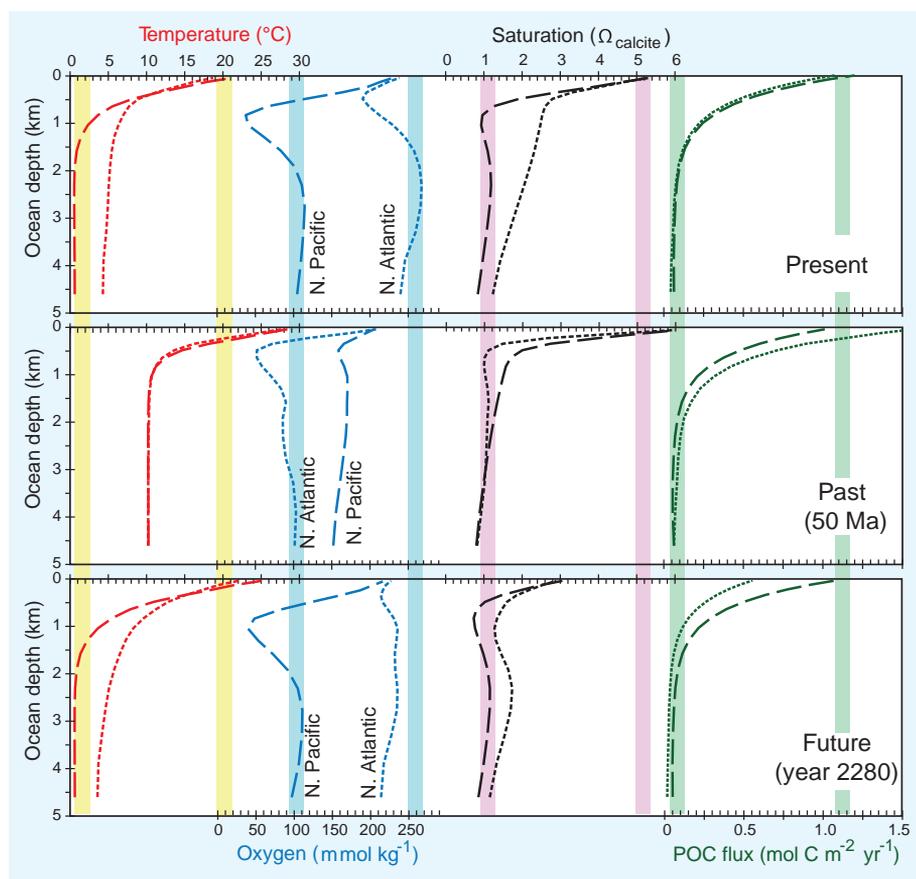


Fig. 6. Dynamics of past, present, and future oceans. Profiles of ocean temperature (red lines), oxygen saturation (blue lines), carbonate ion saturation (black lines), and particulate organic carbon flux (green lines) are shown for modeled averages of the North Pacific (long dashes) and the North Atlantic (short dashes). Note that the future (bottom panel) is a hybrid of the present (top panel) and the past (middle panel). Although the future SST resembles that at 50 Ma, the future deep ocean is much colder, reflecting the continued presence of polar ice and an Antarctic Circumpolar Current. Future oxygenation is reduced in the Atlantic relative to the present, but not as much as in the 50 Ma simulation. Notably, surface ocean carbonate saturation is much lower in the future relative to the present or past, reflecting ocean acidification. Eventually, acidified surface waters will be neutralized by reacting with deep-sea carbonates, reducing deep-sea carbonate concentrations by 10 to 20% (see Fig. 4B). POC flux is model-dependent but shows the expected drop in organic matter export in the future ocean. Colored vertical bands show the maximum and deep ocean minimum values for each parameter. Profiles were generated in cGENIE, with the future simulation the same as in Fig. 4A.



warmth of coming centuries (Fig. 6). Our future Earth model and analogies to the PETM show that a transitional, non-analog set of climates and ecosystems will persist for >10,000 years because of the slow response times of many parts of the biosphere. Over this interval, the oceans will continue to take up CO₂ (from fossil fuel combustion) and heat, causing a rise in sea level, acidification, hypoxia, and stratification. Lessons from the PETM raise the possibility that extinctions in the surface oceans due to greenhouse gas-driven Earth system change will be modest, whereas reef ecosystems and the deep sea are likely to see severe impacts (2). In addition, Earth now supports a much more diverse group of top pelagic predators vulnerable to changes in food chain length (9) than it did in the PETM. The severity and duration of ecosystem impacts due to human greenhouse gas emissions are highly dependent on the magnitude of the total CO₂ addition. If the CO₂ release is limited to historical emissions, ocean surface temperature and carbonate saturation will return close to background within a few thousand years, whereas the “conservative” modeled 2180 Pg C release produces impacts persisting at least 100,000 years (Fig. 4B). Although the future world will not relive the Eocene greenhouse climate, marine ecosystems are poised to experience a nearly continuous state of change lasting longer than modern human settled societies have been on Earth.

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REVIEW

Climate Change and the Past, Present, and Future of Biotic Interactions

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Biotic interactions drive key ecological and evolutionary processes and mediate ecosystem responses to climate change. The direction, frequency, and intensity of biotic interactions can in turn be altered by climate change. Understanding the complex interplay between climate and biotic interactions is thus essential for fully anticipating how ecosystems will respond to the fast rates of current warming, which are unprecedented since the end of the last glacial period. We highlight episodes of climate change that have disrupted ecosystems and trophic interactions over time scales ranging from years to millennia by changing species' relative abundances and geographic ranges, causing extinctions, and creating transient and novel communities dominated by generalist species and interactions. These patterns emerge repeatedly across disparate temporal and spatial scales, suggesting the possibility of similar underlying processes. Based on these findings, we identify knowledge gaps and fruitful areas for research that will further our understanding of the effects of climate change on ecosystems.

Climate change has occurred repeatedly throughout Earth's history, but the recent rate of warming far exceeds that of any previous warming episode in the past 10,000 years (1, 2) and perhaps far longer. Knowledge of how climate change has altered interactions among organisms in the past may help us understand whether consistent patterns emerge that could inform the future of a warming and increasingly human-dominated planet. The fossil record provides an opportunity to study ecosystems on both ecological and geological time scales but is unevenly distributed across time, environments, and taxa and contains only fragmentary information about biotic interactions (3). Modern systems provide direct, though short-term, observational (4) and experimental (5, 6) evidence of changes in biotic interactions during climate change that together can elucidate important mechanisms driving ecological and evolutionary processes. However, it is not always clear how to extrapolate the insights gained from short-term observations over the longer time scales on which future climate change will play out. Robust predictions about the future require multispecies models that combine long-term insights from the past with more specific and shorter-term insights from modern systems—a herculean challenge, given that models for species responses to climate change have only begun to incorporate biotic interactions (7). Even the term “biotic interactions” means different things to different disciplines. We view biotic interactions

in broad terms—namely, as the influence of individuals or populations on one another. In practice, observations from the fossil record and models of the future generally consider the potential interactions of co-occurring species, whereas actual interactions are more easily identified in modern systems. Here we combine insights from past and present-day ecological systems to understand how climate change has affected biotic interactions through time and to identify fruitful avenues for adequately predicting future changes to ecosystems.

How Did Past Climate Change Alter Biotic Interactions?

The geologic record provides unambiguous evidence that some past episodes of climate change have altered biotic interactions by driving extinction and speciation and altering the distributions and abundances of species. The relative diversities of clades and functional groups have varied enormously over geological time [for example, see Fig. 1 for marine genera (8)], and these diversity changes were often accompanied by changes in biotic interactions at both local (9) and global (8, 10) scales. Marine ecosystems, which have the most complete fossil record, exhibit long intervals of relative stability in broad ecological and taxonomic structure, punctuated by short episodes of turnover and ecological upheaval (Fig. 1). These episodes are the well-known mass extinction events (Fig. 1) (11), several of which appear to have resulted from climate change and associated changes such as ocean acidification, eutrophication, and anoxia (12–15).

Mass extinctions illustrate the outcome of complex nonlinear feedbacks between climate change and biotic interactions and offer insights into the types of biotic changes that may be expected in the future. One recurring motif in both marine and terrestrial systems is community homogenization: Mass extinction events are often

followed by the establishment, sometimes for hundreds of thousands of years or longer, of assemblages dominated by ecological generalists with broad environmental ranges. The catastrophic Permian-Triassic (PT) extinction (Fig. 1) demonstrates this phenomenon: Rapid warming and ocean acidification probably caused the extinction of a large proportion of marine (12) and terrestrial (16) taxa, and in both realms post-extinction communities were dominated by ecological generalists (17, 18). Similarly, specialized plant-insect associations recovered much more slowly after the end-Cretaceous mass extinction (Fig. 1) and associated climatic changes (19) than did generalist associations (20).

Mass extinction events may continue to affect the structure of biotic interactions long after ecosystems have recovered to pre-extinction diversity levels. In the case of the PT extinction, the ecosystems that arose after the Early Triassic recovery interval show evidence of increased complexity relative to their pre-extinction analogs (16, 21). For example, in the terrestrial realm some vertebrate groups maintained their pre-extinction functional roles, but entirely new functional groups also emerged, in time giving rise to more complex networks of interactions than existed before the extinction (16). In the marine realm, the PT event profoundly altered the long-term diversity trajectories of major taxa (Fig. 1), and relative abundance distributions imply a lasting post-Permian increase in the ecological complexity of benthic communities (21).

Although mass extinctions provide some of the best evidence for altered biotic interactions, networks of biotic interactions (as implied by the composition of fossil assemblages) also change in ways that do not necessarily involve extinction. Climate-mediated dispersal and invasion events are prominent in the fossil record (22, 23) and may provide valuable analogs for the present. A particularly pertinent example is the Paleocene-Eocene Thermal Maximum 55 million years ago (Ma), when a sudden rise in atmospheric greenhouse gases drove rapid global warming (24). In the Bighorn Basin of North America, this event was associated with compositional changes and novel but transitory species assemblages that emerged after range shifts and the immigration of new species (22). In this same region and time frame, rising temperatures led to increased intensity and frequency of insect herbivory on plants (Fig. 2) (25). The link between insect damage and temperature through time is consistent with modern meridional gradients in herbivore damage diversity (26), suggesting that increased insect herbivory may be a persistent effect of future climate warming (25). The Great American Biotic Interchange, facilitated by a combination of tectonic changes from 12 to 3 Ma that formed the isthmus connecting North and South America and climate-driven changes in habitat along the isthmus, offers another example of large-scale faunal interchange (27). During this event, plants

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probably dispersed between North and South America several million years before animals (28), and rates of evolutionary diversification differed within immigrant mammals in North versus South America (27). These differences in dispersal and diversification among taxa suggest that the arrival of new species into each continent greatly modified existing biotic interactions. Transient, novel assemblages were also a common aspect of latest Pleistocene ecosystems (Fig. 2) (9, 29). The formation of novel plant assemblages in eastern North America (29, 30) appears to have been driven by both taxon-specific range and abundance shifts in response to Pleistocene climate change and ecological release after anthropogenically driven megaherbivore extinction (Fig. 2) (9). The persistence of these communities for almost 2000 years (Fig. 2) suggests that novel

assemblages formed by contemporary and future climate changes may be transitory on geological time scales but long-lived on human time scales.

Whereas changes in the distribution and abundance of species suggest underlying changes in biotic interactions, food web reconstructions inferred from functional morphology (31) or stable isotopes (32, 33) offer more concrete evidence. So far, only a handful of studies have directly evaluated changes in food web structure associated with climate change episodes. One such study suggests that the extinction of some large vertebrate groups during the PT events may have altered the structure of terrestrial food webs in ways that made the generalist-dominated post-extinction recovery communities more prone to ecological collapse (34). Stable isotopic approaches are more feasible in younger assemblages with better preservation

and are a promising area for future research. For example, isotope-based food web models indicate that predator-prey interactions changed with deglacial climate change, with some predators switching prey during the Last Glacial Maximum 21,000 years before the present (yr B.P.) and overall increases in specialization by predators (35).

How Does Contemporary Climate Change Alter Biotic Interactions?

Recent observations and experiments show that climatic changes on the scale of years to decades can change the distributions and abundances of species and alter biotic interactions. As in the past, contemporary climate change may lead to novel, altered, or lost interactions through (local) extinctions, range shifts, and changes in relative abundance (36, 37). For example, with rising tem-

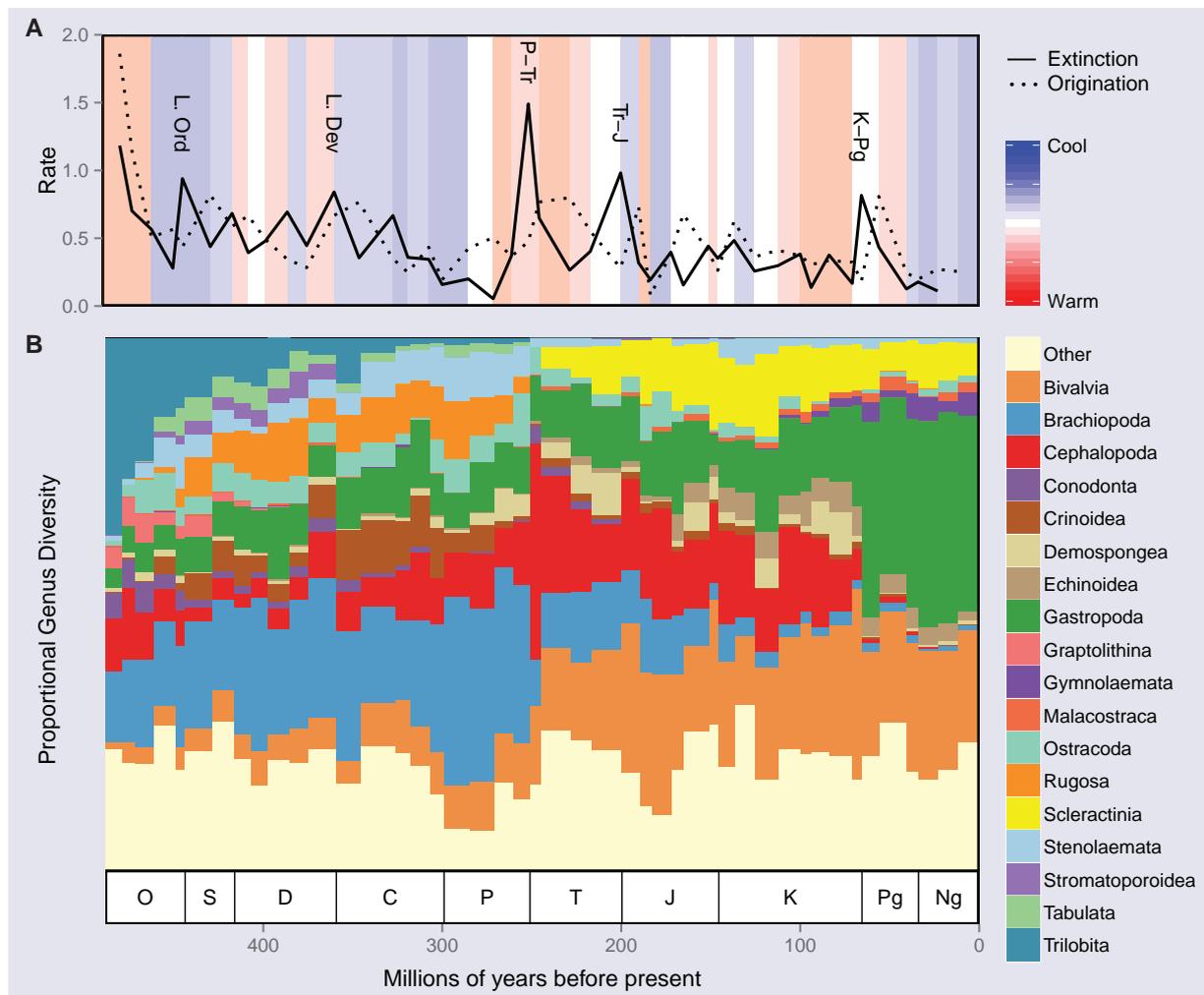


Fig. 1. Macroevolutionary rates and changes in the proportional diversity of fossil marine invertebrate taxa through time and their relationship to broad climate trends. (A) Rates of extinction (solid line) and origination (dotted line) from the Paleobiology Database (8, 85). Colored bands represent relatively warm (red) and cool (blue) intervals and are based on the mean oxygen isotope ratio ($\delta^{18}\text{O}$) of well-preserved marine skeletal carbonates (86) after detrending and rescaling to remove the poorly understood long-term Phanerozoic trend toward

heavier $\delta^{18}\text{O}$ values (86). The “Big Five” mass extinctions are indicated (L. Ord, Late Ordovician; L. Dev, Late Devonian; P-Tr, Permian-Triassic; Tr-J, Triassic-Jurassic; K-Pg, Cretaceous-Paleogene). **(B)** Proportional genus diversity through time, based on genera sampled within each time bin. Age in millions of years before the present and geological periods are indicated along the horizontal axis (O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene).

peratures, species co-occurrence can switch to competitive displacement (38), predation can intensify (39), or new predator-prey interactions can result (40). Fluctuations in climate can also dissipate biotic interactions and allow coexistence by favoring inferior competitors (36). In general, climate change should favor species able to tolerate warmer and more variable climatic conditions, resulting in a relative increase in their performance and/or movement to new locations.

Further complexities arise because feedbacks between biotic interactions and climate can lead

to larger changes in climate and ecosystem function. For example, changing levels of atmospheric CO₂ may alter the relative abundances of different vegetation functional groups such as woody versus nonwoody plants) and in turn affect ecosystem function even further (41). Warming experiments in the Arctic show that higher temperatures favor shrubs (42), and these changes in composition can alter regional climate through changes in albedo and evapotranspiration (43), a feedback that probably occurred during the mid-Holocene 6000 yr B.P. with expanding boreal forests (44).

By 2100, the areal extent of shrubs is expected to expand by 20% (45) to 52% (46) in areas north of 60° latitude, leading to regional temperature increases via decreased albedo and increased evapotranspiration (45, 46).

Higher trophic levels may be most sensitive to climatic change, and both modern and fossil evidence shows that disrupting their trophic interactions can amplify climate changes throughout the community (6, 9, 47). At the same time, experiments in aquatic systems show that warming can intensify trophic cascades, leading to stronger control by top consumers, especially keystone species (39, 48). For example, in pitcher plant communities, top-down controls were stronger with warmer temperatures (49) and in lower-latitude sites than in higher-latitude sites (50). However, climate only accounted for a small amount of the variability in food web structure within these communities along spatial environmental gradients (51). Overall, whether warming promotes or weakens trophic interactions, the results are likely to amplify throughout the community (47).

Climate-driven changes in phenology (the timing of life history events) are especially likely to alter trophic interactions (4), resulting in trophic mismatches (52) and community instability (6). For example, in parts of the Arctic, caribou mediate the effects of warming temperatures on plant functional groups by reducing shrubs and favoring forb production (6). Recent climate change has shifted the peak quality of tundra forage plants to earlier in the year, yet the timing of caribou calving in some regions has not kept pace (52), leading to trophic and phenological mismatches. Similar mismatches and/or new associations during climate change can also result from spatial mismatches due to differences in dispersal ability between interacting species (53). Vagile species are more likely to track changing climate, whereas dispersal-limited species generally are not (54), probably resulting in changes to biotic interactions (36, 53). The superior dispersal ability of a competitor can result in competitive release but also may lead to new competitive matches as novel communities form (37). In turn, these novel interactions could result in further changes to community composition because of a lack of coevolved history (36) (Fig. 3).

Can We Predict Future Biotic Interactions with Climate Change?

Given the interrelationships between climate change, biotic interactions, dispersal, and community composition, models of individualistic species-climate relationships alone will be insufficient to predict future ecological changes (53, 55). For example, adding occurrences of interacting species (prey availability and predator pressure) improved the performance of correlative species distribution models (SDMs) for the arctic fox (*Alopex lagopus*) in Scandinavia (56). Similarly, accounting for dispersal differences and adding a competitor to a SDM helped explain why arctic

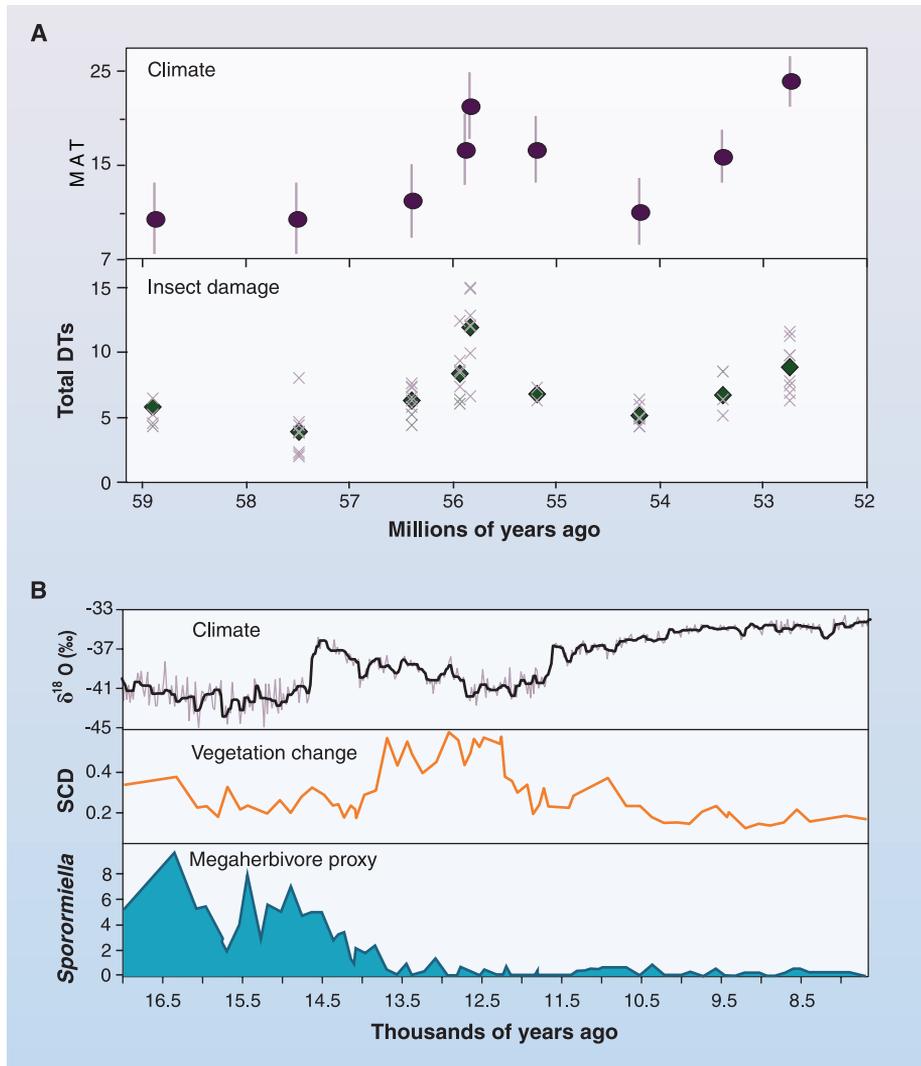


Fig. 2. Biotic interactions through time. (A) The top panel shows an index for mean annual temperature (MAT, ± 1 SD) based on leaf margin analysis, and the bottom panel shows the number of insect damage types (DTs) across the Paleocene-Eocene Thermal Maximum (PETM). Each X symbol represents the number of DTs on a plant host with at least 20 leaves in the flora; the diamonds are the means of the X's at the site [reprinted with permission from (25)]. Insect damage peaked with temperature rise at the PETM. (B) Megafaunal extinction and vegetation change across the Pleistocene-Holocene transition (9). The black line in the top panel indicates $\delta^{18}\text{O}$ from the North Greenland Ice Core Project (87). The orange line represents the minimum squared chord dissimilarity (SCD), indicating the dissimilarity of vegetation from that of the present. The blue line represents the abundance of the dung fungus *Sporormiella*, as a percentage of the upland pollen sum, which represents the presence or absence of megafauna. Vegetation dissimilarity peaked after local megafaunal extinction [reprinted with permission from (9)].



char (*Salvelinus alpinus*) may not expand into climatically suitable lakes as temperatures warm in the future (57).

Despite promising results from SDMs that include biotic as well as climatic predictors, there is a clear need to develop and validate more process-based methods that incorporate multi-species interactions, dispersal, and community assembly to predict communities of the future. Recent work suggests that this might best be realized by examining spatial and temporal patterns of species co-occurrence along environmental gradients (58) and by developing dynamic macroecological models that consider patterns of co-occurrence while incorporating (implicitly or explicitly) important ecological processes (59). Although a paucity of spatiotemporal co-occurrence data may challenge the parameterization and validation of such models (55), the relatively data-rich Quaternary (2.588 Ma to the present) represents an important exception. Pooling data across time may provide more robust estimates of species-climate relationships (60–62) and could distinguish species associations that arise because of similar environmental constraints from those due to tightly linked biotic interactions (63). Simplifying communities to assemblages of functional groups or traits may also help develop robust predictions that translate across time scales (64).

Opportunities for Synthesis

Whereas increased understanding of the ways in which climate change influences biotic interactions is key to making predictions about the future (36, 65), substantial challenges remain. A crucial difference between the past and the future is the degree of human alteration of ecosystems. Humans already influence more than 80% of Earth's land surface (66), and by 2100, when human population size is expected to double that of today, a quarter or more of the planet could experience climatic conditions that have no modern analog (67). The combination of climate change, human land use, and unsustainable harvests may ultimately lead to extinction rates rivaling those of major mass extinctions in the geological past (68). Mass extinctions have strongly affected the form and nature of ecosystems throughout time; given the interaction of diverse anthropogenic drivers today and in the future, and especially when considered alongside the ongoing global exchange and spread of invasive species, a future mass extinction event could be accompanied by community reorganization, homogenization, and ecological novelty on an unprecedented scale.

How, then, do we move forward toward a better understanding of the future of biotic interactions? Both the past and present provide important insights regarding the influence of climate change on biotic interactions. We highlight four areas of promising synthesis across time scales that can help anticipate changes in the future: (i)

compile baselines for the relative frequency of specialized versus generalized interactions through time; (ii) elucidate the role of dispersal in mediating changes in biotic interactions; (iii) focus on time-invariant metrics such as interactions between functional groups rather than species; and (iv) use the rich and high-resolution paleoclimatic and ecological data from the Quaternary as a bridge between the ecological time scales of the present and the evolutionary scales of deep time.

Across time scales, we lack baselines for the relative frequency of specialized versus generalized interactions and how that frequency will shift with climate change. For example, a long-held theory in ecology is that specialized interactions should be most prevalent in stable environments, where time and stability allow such tightly co-evolved interactions to arise and persist (69). In contrast, generalized interactions should dominate regions that have experienced rapid environmental change. Current global biogeographical patterns support these predictions (70), and regions where climate fluctuated more strongly during the Quaternary show community structures consistent with a history of disrupted spe-

cies interactions (71). Additionally, generalist taxa (72) and interactions (20) often dominated assemblages after rapid past climate change. When extrapolated to the rapidly changing conditions of the future, tightly coevolved interactions— notably mutualism and parasitism—could be under greatest threat (36, 73). Given the projected combination of highly novel environments (67) with increasing impacts from other anthropogenic drivers (74), rapid biotic turnover, especially where weedy species and pathogens are poised to invade disturbed or weakly coevolved systems, may result in the formation of communities and ecosystems very different from those on Earth today (Fig. 3) (75). The combined impacts of extinction and invasion also mean that communities will become increasingly homogeneous in the future (76), at least on short evolutionary time scales. However, key issues need to be resolved before we can fully generalize this prediction. First, the definition of what constitutes a “generalist” or “weedy” species or interaction needs to be reconciled across paleo and modern systems. Second, limited evidence from mass extinction events suggests that more-complex ecosystems emerge after the transient rise of generalist taxa,



Fig. 3. Climate change and biological invasions alter the distribution and abundance of species, resulting in novel species combinations and interactions between organisms with no previous history of association. (A) Recent increases in minimum winter temperature have allowed the palm *Trachycarpus fortunei* to escape cultivation and invade the deciduous forest of southern Switzerland, far north of other viable palm populations (88) [photo credit: M. C. Fitzpatrick]. Novel interactions between species can sometimes cause dramatic and unpredictable changes in ecosystems. By removing the dominant native omnivore, the red land crab (*Gecarcoidea natalis*), and by increasing the populations of two scale insects (*Tachardina aurantiaca* and the nonnative *Coccus celatus*), the invasion of the yellow crazy ant (*Anoplolepis gracilipes*) on Christmas Island altered three trophic levels and led to shifts in the island's rainforest ecosystems from (B) an open to (C) a dense understory (89) [photo credit: P. T. Green]. Symbols are used courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols/).

but whether this pattern holds at other times in the past and whether it emerges on shorter time scales are unknown. Overall, knowledge about the temporal evolution of biotic interaction baselines would itself be highly informative and would also provide the foundation for assessing future changes in biotic interactions.

Another theme that is consistent through time is that novel biotic interactions often arise in rapidly changing environments (9, 22, 37, 77) and that dispersal may play a key role in mediating these changes in biotic interactions. Even though contemporary and fossil evidence shows that dispersal differences and biotic interactions can combine to mediate species' responses to climate change (23, 30, 53, 54), more research is needed to make explicit links between dispersal and biotic interactions through time. A first step toward this goal would be to examine patterns of species co-occurrence across space and time and determine to what extent the stability of those patterns differs between vagile and dispersal-limited taxa. Related, the geographic distributions of numerous taxa shifted substantially during the late Quaternary, and most studies have attributed these changes to individualistic responses governed primarily by environmental constraints (78, 79). However, for range shifts that are not fully explained by climate change, the extent to which the mismatch is due to dispersal limitation versus concerted responses stemming from biotic interactions [or both (53)] is unclear (30, 54).

The widely disparate observational time scales of the past and the recent present hinder full realization of these emerging insights (80), but this problem in part can be ameliorated by controlling for the amount of time across which rates of biotic and climate change are calculated (68). Although we lack direct knowledge of the detailed ecology of many extinct species, recent studies have shown that a focus on taxon-free metrics such as functional groups or traits can be informative in making comparisons across time intervals (34, 64). An important next step is to extend these efforts to the responses of biotic interactions to climate change across time scales. Similarly, metrics such as community or food web structure that are relatively independent of particular species can provide a "common currency" [(77); (81), p. 747] and framework for discussing future community and ecosystem changes that translate irrespective of time scales (82).

For all of these challenges, further study of the Quaternary record will be of paramount importance. The Quaternary fossil record serves a central role in bridging from the ecological time scales of the present to evolutionary scales seen in deep time. This record is data-rich, and for some systems or sites, time scales of change can be resolved to decades or less (83). Climate changes during this period are relatively well understood from independent evidence and models (84) and include multiple glacial-interglacial cy-

cles. Quaternary assemblages typically contain many extant species, and genetic and isotopic data are available for many species and assemblages (35, 78). Multiple lines of evidence can be used to evaluate the effects of specific climatic drivers on the structure of biotic interaction networks at multiple spatial and temporal scales. Comparisons between modern and Quaternary systems can help illuminate mechanisms and test the generality and permanence of short-term patterns [for example, by teasing apart the roles of climate, CO₂, and fire in functional shifts in vegetation type (41)]. Similarly, comparisons between the Quaternary and older intervals can test whether patterns observed on comparatively short time scales hold across longer intervals and elucidate the circumstances under which ecological changes translate into evolutionary change [for example, comparing current and expected future extinction rates to mass extinction events (10, 68)]. A detailed examination of the Quaternary fossil record will be key to integrating insights from fossil and extant systems and, ultimately, improving our ability to anticipate the effects of climate change on ecosystems in the future.

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REVIEW

The Future of Species Under Climate Change: Resilience or Decline?

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As climates change across already stressed ecosystems, there is no doubt that species will be affected, but to what extent and which will be most vulnerable remain uncertain. The fossil record suggests that most species persisted through past climate change, whereas forecasts of future impacts predict large-scale range reduction and extinction. Many species have altered range limits and phenotypes through 20th-century climate change, but responses are highly variable. The proximate causes of species decline relative to resilience remain largely obscure; however, recent examples of climate-associated species decline can help guide current management in parallel with ongoing research.

A better understanding of how species respond to ongoing anthropogenic climate change is crucial for assessing vulnerability and guiding efforts to avoid potentially severe biodiversity loss (1, 2). However, whereas forecasts of changes in species’ geographic ranges typically predict severe declines (3, 4), paleoecological studies suggest resilience to past climatic warming (Fig. 1) (5–7). Superficially, it seems that either forecasts of future response are overestimating impacts (8) or that history is somehow an unreliable guide to the future (9). Here, we explore the apparent contradiction between (observed) past and (predicted) future species responses by first summarizing salient concepts and theory, then reviewing (i) broad-scale predictions of future response and (ii) evidence from paleontological and phylogeographic studies of

past responses at millennial or greater time scales. To bridge the two, we consider evidence for responses to more recent (20th-century) climate change. Finally, we place these observations in a management context.

What Theory Says: Concepts and Predictive Models

In principle, the vulnerability of a given species to climate change is a combination of exposure (that is, regional or “mesoscale” change in climatic means and extremes) and intrinsic sensitivity (for example, due to physiological limits, habitat or trophic specialization, life history characteristics, or obligate species interactions). These factors are mediated by response, defined as the capacity of local populations to buffer climatic alterations in situ via plastic reactions (including behavioral responses) or genetic adaptation, or by shifting geographically to track optimal conditions (Fig. 2A) (1, 2, 10).

Exposure is typically measured as shifts in mean precipitation or temperature at the mesoscale (e.g., 1 to 100 km²). For temperature, ensemble forecasts tend to predict the largest increases in northern high latitudes and the lowest across

the southern oceans (11). Novel climatic conditions, in which new species assemblages might form, are predicted for the tropics, with disappearing climates in the mountains (12). The expected increase in frequency of extreme climate events will probably also affect species persistence (13, 14). An important consideration here is how landscape features such as slope, aspect, vegetation cover, and soil moisture can ameliorate shifts in means and extremes of temperature at the microenvironmental scale that organisms actually experience (1, 15–19). In this context, topographically complex areas provide potential climate change refugia (microrefugia) (19–22), whereas low-relief topography can exacerbate climate change impacts, as organisms must move further to remain in the same climate space (23). In lowland areas, the requirement to move larger distances to track climate, especially if combined with dispersal limitation due to habitat fragmentation, can cause a lag in the response, possible leading to lowland biotic attrition with important changes in ecosystem functioning (24).

A key dimension of species’ response is the capacity to persist in situ by altering fitness-related traits by plastic change or genetic adaptation. Plastic responses are undoubtedly important for short-term persistence (25, 26), but they can also entail costs (27) and may be insufficient to avoid extinction (28). Evolutionary rescue requires moderate-to-high heritability of key traits and/or high potential growth rates of populations, with critical levels of these parameters increasing with the rate of change (29–31) (Fig. 2B). All of the above is subject to fitness trade-offs across genetically correlated traits, which can further constrain evolutionary response (32). So far, and despite abundant evidence for adaptive variation across contemporary climatic gradients, direct evidence of genetically based adaptation to climate change over time remains sparse (33–36).

Perhaps the greatest potential for species to respond to climate change rests with local shifts in microhabitat use and dispersal to track suitable

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REVIEW

The Future of Species Under Climate Change: Resilience or Decline?

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As climates change across already stressed ecosystems, there is no doubt that species will be affected, but to what extent and which will be most vulnerable remain uncertain. The fossil record suggests that most species persisted through past climate change, whereas forecasts of future impacts predict large-scale range reduction and extinction. Many species have altered range limits and phenotypes through 20th-century climate change, but responses are highly variable. The proximate causes of species decline relative to resilience remain largely obscure; however, recent examples of climate-associated species decline can help guide current management in parallel with ongoing research.

A better understanding of how species respond to ongoing anthropogenic climate change is crucial for assessing vulnerability and guiding efforts to avoid potentially severe biodiversity loss (1, 2). However, whereas forecasts of changes in species’ geographic ranges typically predict severe declines (3, 4), paleoecological studies suggest resilience to past climatic warming (Fig. 1) (5–7). Superficially, it seems that either forecasts of future response are overestimating impacts (8) or that history is somehow an unreliable guide to the future (9). Here, we explore the apparent contradiction between (observed) past and (predicted) future species responses by first summarizing salient concepts and theory, then reviewing (i) broad-scale predictions of future response and (ii) evidence from paleontological and phylogeographic studies of

past responses at millennial or greater time scales. To bridge the two, we consider evidence for responses to more recent (20th-century) climate change. Finally, we place these observations in a management context.

What Theory Says: Concepts and Predictive Models

In principle, the vulnerability of a given species to climate change is a combination of exposure (that is, regional or “mesoscale” change in climatic means and extremes) and intrinsic sensitivity (for example, due to physiological limits, habitat or trophic specialization, life history characteristics, or obligate species interactions). These factors are mediated by response, defined as the capacity of local populations to buffer climatic alterations in situ via plastic reactions (including behavioral responses) or genetic adaptation, or by shifting geographically to track optimal conditions (Fig. 2A) (1, 2, 10).

Exposure is typically measured as shifts in mean precipitation or temperature at the mesoscale (e.g., 1 to 100 km²). For temperature, ensemble forecasts tend to predict the largest increases in northern high latitudes and the lowest across

the southern oceans (11). Novel climatic conditions, in which new species assemblages might form, are predicted for the tropics, with disappearing climates in the mountains (12). The expected increase in frequency of extreme climate events will probably also affect species persistence (13, 14). An important consideration here is how landscape features such as slope, aspect, vegetation cover, and soil moisture can ameliorate shifts in means and extremes of temperature at the microenvironmental scale that organisms actually experience (1, 15–19). In this context, topographically complex areas provide potential climate change refugia (microrefugia) (19–22), whereas low-relief topography can exacerbate climate change impacts, as organisms must move further to remain in the same climate space (23). In lowland areas, the requirement to move larger distances to track climate, especially if combined with dispersal limitation due to habitat fragmentation, can cause a lag in the response, possible leading to lowland biotic attrition with important changes in ecosystem functioning (24).

A key dimension of species’ response is the capacity to persist in situ by altering fitness-related traits by plastic change or genetic adaptation. Plastic responses are undoubtedly important for short-term persistence (25, 26), but they can also entail costs (27) and may be insufficient to avoid extinction (28). Evolutionary rescue requires moderate-to-high heritability of key traits and/or high potential growth rates of populations, with critical levels of these parameters increasing with the rate of change (29–31) (Fig. 2B). All of the above is subject to fitness trade-offs across genetically correlated traits, which can further constrain evolutionary response (32). So far, and despite abundant evidence for adaptive variation across contemporary climatic gradients, direct evidence of genetically based adaptation to climate change over time remains sparse (33–36).

Perhaps the greatest potential for species to respond to climate change rests with local shifts in microhabitat use and dispersal to track suitable

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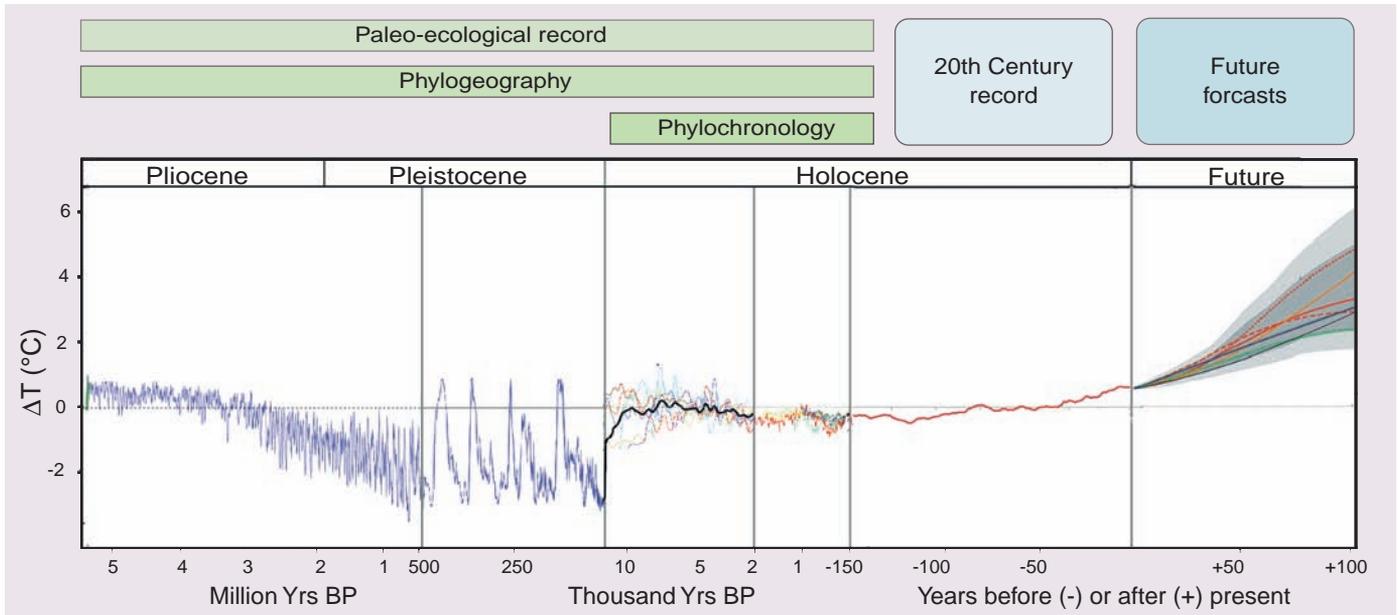


Fig. 1. Global mean temperate fluctuations and scales of inference across the historical record and future predictions. The paleoclimate record is modified from http://commons.wikimedia.org/wiki/File:All_palaeotemps.png, data for the 20th-century record were obtained from http://data.giss.nasa.gov/gistemp/graphs_v3/, and forecasts of future change are adapted

from (107), figure SPM.5 (different colors represent predictions under different models). Note the differences in scale on the x axis and that forecasts under higher-emission scenarios exceed the natural variability observed over the historical record. ΔT , change in temperature; Yrs BP, years before the present.

climatic conditions. Species that actively thermo-regulate may be able to select microhabitats that are buffered from extreme conditions (20, 37), though this can also restrict activity, which may lead to local extinction (38). This aspect of response to climate change has not been studied sufficiently and warrants greater attention. Dispersal to track geographic shifts in climate is clearly the dominant response measured from paleontological and 20th-century records (see below). The scale of dispersal required is a function of both the regional magnitude of climate change and topography, combined with the species sensitivity (23).

Predicted Impacts of Future Climate Change

Forecasts of potential species responses to future climate change come in two varieties: (i) correlative or mechanistic models of individual species (39) or (ii) prediction of higher-level properties such as species richness (3) or turnover (40). Correlative models are currently the most widespread and scalable method (41), but they have inherent limits. These models typically apply some form of climate envelope approach, assessing whether the (realized) climate niche occupied by a species continues to exist within the current geographic range and whether it will shift elsewhere or cease to exist. This approach has often been criticized for lacking a direct mechanistic basis and the inherent danger of extrapolation (9). Additionally, these models are generally computed at a coarse spatial resolution and fail to capture spatial variability in temperature over

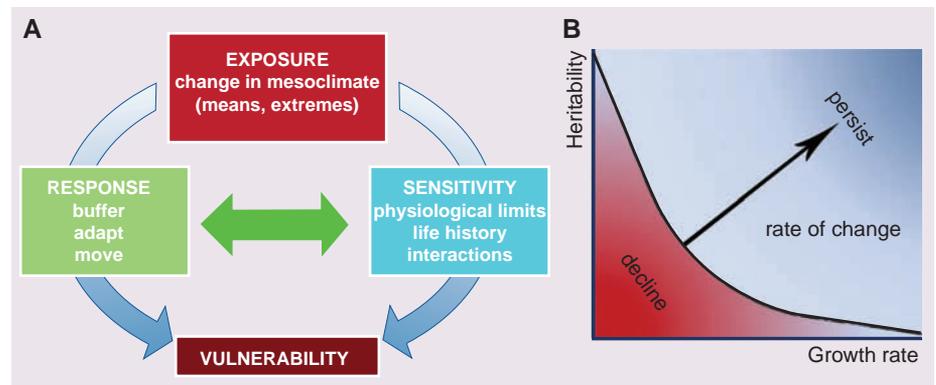


Fig. 2. Factors affecting species vulnerability to climate change. (A) Schematic of the pathway from exposure to broad-scale climate change to species vulnerability [see (1, 2) for analogous representations]. (B) Limits to evolutionary rescue imposed by trait heritability, the intrinsic rate of population growth, and the rate of change in the environment (e.g., temperature). This schematic is modified from (36) and is based on theoretical models in (29).

tens to hundreds of meters, at which the buffering role of microhabitat heterogeneity may be crucial for species persistence (18, 42). Thus, correlative models are probably a better measure of exposure than of species vulnerability to climate change.

The actual predictions of effects on species persistence are often dire, however. For example, one prominent analysis predicted that 15 to 37% of species would be endangered or extinct by 2050 (3). Another predicts more than a 50% loss of climatic range by 2080 for some 57% of widespread species of plants and 34% of animals (4). Montane taxa are expected to lose range area

as they shift upward with warming. Again, predicted effects are catastrophic (43–45) and could be even worse for the highly endemic biotas of tropical montane forests if the cloud base lifts (46). For the tropical lowlands, high levels of species attrition are predicted because of narrower physiological tolerances (47) and a high velocity of change due to shallow temperature gradients (48). Reduction of species ranges is expected to result in substantial loss of geographically structured genetic variation, perhaps including cryptic taxa (49, 50). Yet, we must acknowledge the level of uncertainty of these predictions and the possibility that these



models are overestimating extinction risk. Future models should be improved by incorporating key parameters such as finer-scale topographic heterogeneity (18), interaction of biotic (51, 52) and other anthropogenic factors (7, 45, 53), species physiological constraints and plastic acclimation capacity (39), as well as demographic processes [see for instance, the recent findings of Reed *et al.* (54) in a wild population in which density-dependent compensation counteracts the reduced fledgling rates due to phenological mismatch provoked by climate change].

What the Data Say: Species Responses to Past Climate Change

The Paleocological Record

The fossil record and the imprint of history in geographic patterns of DNA diversity (phylogeography) provide valuable insights into how species responded to past shifts in global temperature, including rapid warming events at the Pleistocene-Holocene transition (Fig. 1). These sources of information on historical responses have distinct limitations that can be partially overcome by combining types of evidence (see below). The fossil record varies in extent and resolution according to preservation conditions (55, 56); that is, a sparse faunal record for the tropics; underrepresentation of small, rare, and physically fragile species; and, sometimes, low taxonomic resolution (i.e., identification to genus rather than species). Phylogeographic analysis, on the other hand, affords higher spatial resolution but typically has low temporal precision compared with fossils.

The picture emerging from fossil evidence, including the Pleistocene-Holocene transition, is one of both robustness and dynamism. To simplify, there was no signal of elevated extinction through periods of rapid change (5, 6, 57), and, at the level of genera, composition and trophic

structure of mammalian communities appear robust [(5), but see (58)]. One exception is recent megafaunal extinctions, where climate change and human impacts likely combined with devastating consequences (59, 60). This is not to say that the biota was static through past climate change—far from it. The dominant response was idiosyncratic shifts in geographic range (61–63) with concomitant shuffling of community composition, often resulting in nonanalog assemblages (9). Geographic shifts are well described for mammals and appear more pronounced for habitat or dietary specialists than generalists (5, 64, 65). Another type of response described well in mammals through past warming periods is decrease in body size, a key ecological trait (5, 66).

Comparative phylogeographic studies, often combined with paleoclimatic modeling of geographic ranges, offer another window on past species responses (67) and can identify regions in which taxa persisted through past climate change; that is, evolutionary refugia (68–70). Again, such studies point to disparate species' responses, with some evidently persisting in many areas and others in just a few major refugia, despite a common history of climate change across the focal landscape (71–74). When combined with fossil evidence and spatial models, such studies highlight the extent of range shifts but also the importance of scattered microrefugia, which are important for range recovery (6, 75) and perhaps also harbor distinct adaptations (76, 77). Going further, direct DNA analyses of subfossils provide a much clearer picture of population dynamics through climate change (78) and, for megafauna, highlight differences among species in response to the twin challenges of climate change and human colonization (7, 79).

The 20th-Century Record

The discord between predictions of high extinction under future climate change and relatively

high resilience through paleoclimatic change could be partly due to the limitations of the fossil record (see above) but may also reflect the fact that, with the possible exception of Holocene megafauna, species were previously able to respond in the absence of other human-caused impacts on natural systems. Thus, even though the rate of expected future change may be much faster than that over the past century, there is value in examining how species have responded to climate change over the 20th century.

There is abundant evidence for climate-related changes in distributions and timing of life history events of species over the past decades. Meta-analyses across thousands of species report strong trends in shifts of geographic range limits, predominantly toward higher latitudes and higher elevations for terrestrial taxa and lower depths for marine taxa, as expected in a warming world (80–82). These trends are reflected even in increasing representation of more tropical species in major fisheries (83). Recent climate change has also affected the communities' composition by increasing the dominance of generalist taxa and larger basal prey species, whereas habitat specialists, rare species, and species with more northerly distributions have declined (84–87).

Yet again, a dominant feature is marked heterogeneity of species responses. For example, Chen *et al.* (80) report that about one-quarter of species moved downhill or toward lower latitudes, opposite of what was expected. This observation may reflect marked differences in 20th-century climate change across regions and between marine and terrestrial systems (88). However, the same is seen within a single biome [e.g., UK terrestrial species (80)]. To take one example, studies across strong environmental gradients in California revealed both upward and downward shifts in plants (89) and birds (90), whereas montane small mammals mostly shifted upward, in accord with increasing minimum temperatures and lead-

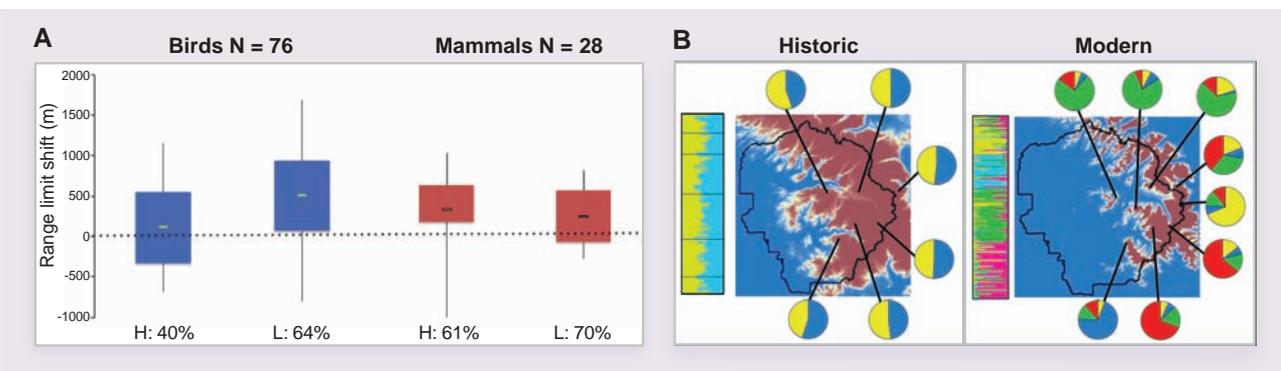


Fig. 3. Species responses to 20th-century climate change. (A) Examples of heterogeneity of shifts in range limits for small mammals and birds across Yosemite National Park, California, and across a century of environmental change. H, lower limit of high-elevation species; L, upper limit of low-elevation species; both are displayed with the percentage of species showing significant

range shifts. Data are from (90, 91). **(B)** Decreased extent and increased fragmentation of the range of the alpine chipmunk (*Tamias alpinus*) across Yosemite, with a concomitant increase in genetic structure associated with the upward contraction of this montane specialist from the early 20th century to the present. Modified from (108).

ing to substantial range contractions (91) (Fig. 3). Yet even closely related species (e.g., different species of chipmunk, voles, or field mice) showed disparate responses. Lenoir *et al.* (92) summarize some of these examples and suggest habitat modification, as well as species interactions and their interplay with climate change, as possible mechanisms explaining the observed variability. These observations highlight the complexity of the process and the difficulty of accurately predicting future effects based on actual models. This points to the need for a more nuanced approach to predicting species vulnerability—one that also considers changes in precipitation, productivity, and habitat structure (89, 90). It is difficult to identify traits that predict whether or not species will track temperature change (93). Species expanding ranges upward or to higher latitudes tend to be weedy, prolific, and/or ecological generalists (86, 87, 91, 94). But as yet, few, if any, traits provide robust prediction of which species are observed to contract in range. It is the latter we should be most concerned about.

Shifts in phenology (e.g., earlier flowering, breeding, and migration and reduced migration) are also widely observed in the 20th-century record and could cause temporal mismatch between strongly interacting species, especially where these species employ different environmental cues (28, 95, 96). As expected with warming, decreasing body size has been observed in several studies of birds and mammals (97). This response seems to be plastic rather than genetic (98, 99), or it may be related to extended food availability rather than direct physiological effects (100). Again, idiosyncrasy is the trend; some hibernating mammals show increasing body size, perhaps due to a longer period of food availability (100, 101). Finally, as yet, no species extinctions are clearly attributable to climate change per se, although several studies recorded local extinctions and population declines (102). Nevertheless, it is very difficult to establish causative relationships between warming and population declines or extinction, due to the interaction with other anthropogenic factors such as habitat loss or previously unseen pathogens [e.g., declines of amphibians in the montane neotropics (103, 104)]. A recurring message is that we have insufficient knowledge of the proximate cause(s) of observed species declines under global warming: The few examples appear to be more closely related to indirect ecological effects than to demonstrable physiological challenges (102).

Management in the Face of Change and Uncertainty

The historical record over millennia and the past century demonstrates that species do respond to climate change, albeit in ways difficult to predict individually. As we move into climate conditions without recent parallel and across ecosystems already strongly affected by humans, the challenge is to increase resilience of natural systems now, in

conjunction with continuing research to improve our capacity to predict vulnerability (1, 2). These priorities must undoubtedly be accompanied by the urgent mitigation of the main culprit, the greenhouse gas emissions (4).

What Do We Know?

The simplest and most strongly supported response of species is to shift geographically to track their climatic niche. Observed responses to paleoclimatic change emphasize the importance of refugia—both macro- and microrefugia (16)—as key landscapes to protect.

Given rapid climatic change, evolutionary rescue of intrinsically sensitive species is most plausible for those with short generation times and high potential population growth. In particular, for potentially sensitive species with long generation times, every effort should be made to minimize other stressors on population viability and to monitor population trends.

Taken together, managing and restoring evolutionary dynamics across large ecologically heterogeneous landscapes, including long-term climatic refugia, and enabling habitat connections to these refugia are increasingly acknowledged as priorities. Recognizing that species and ecosystems are naturally dynamic and are likely to become more so with anthropogenic impacts, maintaining the status quo should not be the conservation goal; rather, we should seek to manage system dynamics within bounds to avoid large-scale state changes (105, 106).

What Don't We Know? Some Research Priorities

Understanding and predicting the effects of future climate change on species, let alone communities and ecosystems, is an urgent and fundamental challenge to this generation of biologists. Although we have identified many areas of uncertainty and more can be found in the broader literature, we will now highlight just three areas of immediate relevance to conservation decision-makers.

First, understanding the capacity of species to buffer effects of climate change *in situ* is crucial if we are to predict and manage vulnerable species. Key aspects include better understanding of the limits of plasticity of key traits and microhabitat buffering. Along the same lines, aside from some generalizations, research on trait-based prediction of vulnerability has a long way to go before it can provide a robust management tool. Progress on these aspects will come from intensive analyses of the proximate causes of climate-related species decline, as well as further comparative studies.

Second, predictive models of spatial and demographic responses of species must be tested and improved, yet must also remain scalable to many species. Parameter-rich models incorporating demography, dispersal, intrinsic limits, and evolutionary response are ideal and can be applied to model systems. The identification of generalizations and hybrid approaches will enable

more robust predictions for larger numbers of less well known species.

Third is the vexing problem of species interactions: Do tipping points exist and lead to irreversible state change (52, 105)? How do we reconcile these concerns with evidence for dynamism of communities and resilience of trophic structure through past climate change?

Underpinning all of the above is the need to make greater use of the record of the responses to past climate change, over time scales from millennia to decades. The potential of museums and herbaria collections and records is becoming more apparent, but much more needs to be done to capture and apply the invaluable data and field notes from long-term studies of 20th-century ecologists.

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REVIEW

Climate Change Impacts on Global Food Security

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Climate change could potentially interrupt progress toward a world without hunger. A robust and coherent global pattern is discernible of the impacts of climate change on crop productivity that could have consequences for food availability. The stability of whole food systems may be at risk under climate change because of short-term variability in supply. However, the potential impact is less clear at regional scales, but it is likely that climate variability and change will exacerbate food insecurity in areas currently vulnerable to hunger and undernutrition. Likewise, it can be anticipated that food access and utilization will be affected indirectly via collateral effects on household and individual incomes, and food utilization could be impaired by loss of access to drinking water and damage to health. The evidence supports the need for considerable investment in adaptation and mitigation actions toward a “climate-smart food system” that is more resilient to climate change influences on food security.

Tackling hunger is one of the greatest challenges of our time (1). Hunger has multi-dimensional dimensions and causes, ranging from

deficiencies in macro- and micro-nutrients, through short-term shocks on food access, to chronic shortages. Causes range from constraints on the supply

of food of sufficient quantity and quality and lack of purchasing power to complex interactions of nutrition with sanitation and infectious diseases leading to poor health. Several of these causes have been addressed in recent decades, and substantial progress has been made in reducing the proportion of the world’s undernourished population from an estimated 980 million in 1990–92 to about 850 million in 2010–12 (2). However, from other relevant indicators of nutrition, such as child underweight and stunting and health surveys, an estimated 2 billion people still suffer from micro-nutrient deficiencies today.

The long-term reduction in the prevalence of undernutrition worldwide has slowed since 2007, as a result of pressures on food prices, economic

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volatilities, extreme climatic events, and changes in diet, among other factors. Furthermore, additional pressures on the global food system are expected to build in the future. For example, demand for agricultural products is estimated to increase by about 50% by 2030 as the global population increases (3), which will require a shift toward sustainable intensification of food systems (4). The impacts of climate change will have many effects on the global food equation, both for supply and demand, and on food systems at local levels where small farm communities often depend on local and their own production (5). Thus, climate change could potentially slow down or reverse progress toward a world without hunger.

Here, we offer an overview of the evidence for how climate change could affect global food security, with particular emphasis on the poorer parts of the world. We deliberately take a broad view of the complex interactions between climate change and global food security, stating what we do know with some degree of confidence, as well as acknowledging aspects where there is little or no evidence. We end by proposing a number of precepts for those making policy or practical decisions on climate change impacts and food security.

Food Security

Together, climate change and food security have multiple interrelated risks and uncertainties for societies and ecologies. The complexity of global

food security is illustrated by the United Nations' Food and Agricultural Organization (FAO) (6) definition: (i) the availability of sufficient quantities of food of appropriate quality, supplied through domestic production or imports; (ii) access by individuals to adequate resources (entitlements) for acquiring appropriate foods for a nutritious diet; (iii) utilization of food through adequate diet, clean water, sanitation, and health care to reach a state of nutritional well-being where all physiological needs are met; and (iv) stability, because to be food secure, a population, household or individual must have access to adequate food at all times.

It is extremely challenging to assess precisely the current status of global food security from such a broad concept. However, the big picture is clear: About 2 billion of the global population of over 7 billion are food insecure because they fall short of one or several of FAO's dimensions of food security. Enormous geographic differences in the prevalence of hunger exist within this global estimate, with almost all countries in the most extreme "alarming" category situated in sub-Saharan Africa or South Asia (7) (Fig. 1).

Nevertheless, it is important to note that the current numbers for undernourished people are rough estimates at best and are seriously deficient in capturing the access, utilization, and stability dimensions of food security. First, the methods used to make these estimates only cap-

ture longer-term trends, not the short-term changes that can be an important consequence of climate variability. The most recent data are averages for the period 2010–2012 (2), so they do not capture a specific year, let alone shorter-term shocks, be they climate-related or otherwise. Second, they estimate calorie shortage only and do not cover other dietary deficiencies and related health effects that can impair physical and mental capacities. Third, they are derived from aggregate data, not actual household or individual-level food deficiencies, which hinders analyses of distributional effects of climate and other shocks. The FAO methodology was recently improved (8), but the above shortcomings could not be addressed within the framework of the current method, and thus, current analyses of climate change impacts on food security are incomplete. An overhaul of data-gathering methods that encompasses food deficiencies at household levels, as well as nutritional status, is needed.

Climate Change

There is a substantial body of evidence that shows that Earth has warmed since the middle of the 19th century (9–14). Global mean temperature has risen by 0.8°C since the 1850s, with the warming trend seen in three independent temperature records taken over land and seas and in ocean surface water (15). Climate change can result from natural causes, from human activities

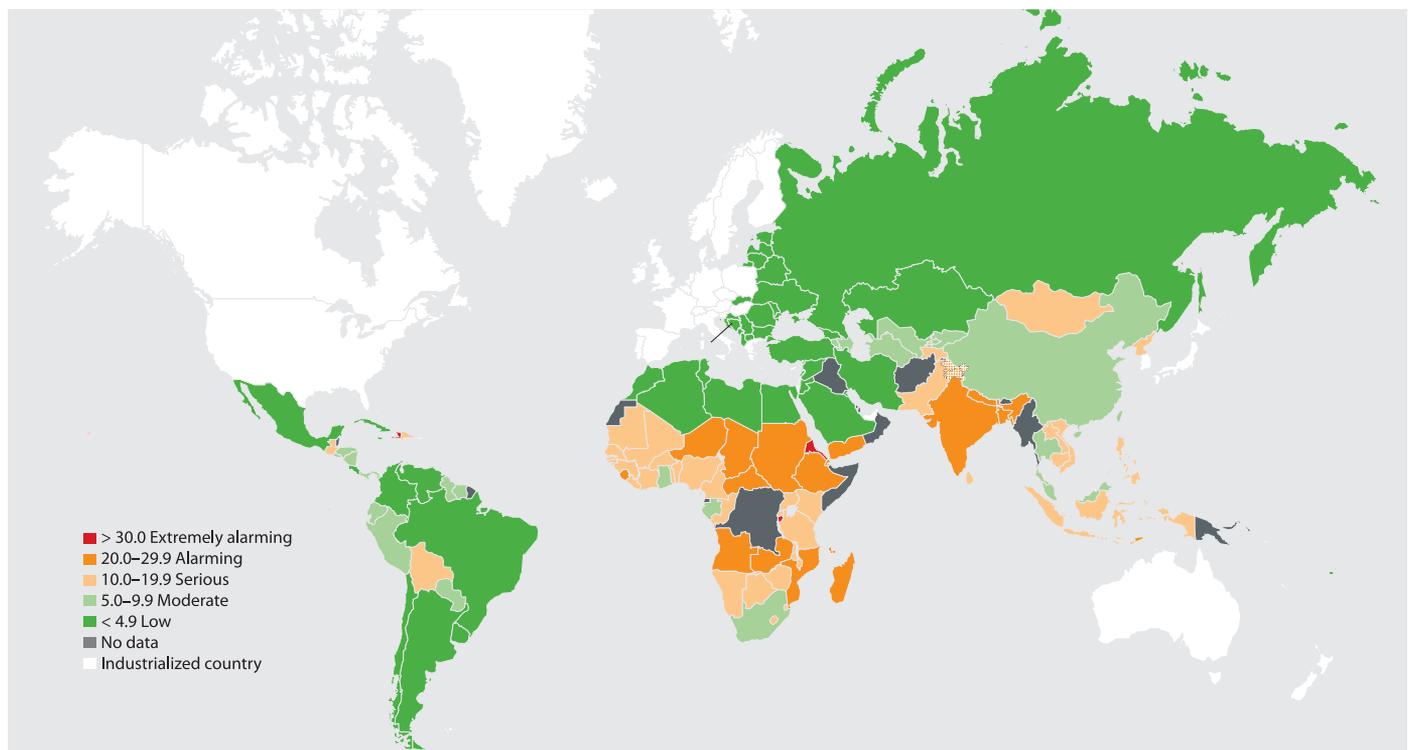


Fig. 1. Global distribution of hunger as quantified by the 2012 Global Hunger Index. The Welthungerhilfe, IFPRI, and Concern Worldwide Hunger map 2012 calculated a Global Hunger Index (7) for 120 countries by using the proportion of

people who are undernourished, the proportion of children under 5 who are underweight, and the mortality rate of children younger than age 5, weighted equally. [Reproduced with permission from Welthungerhilfe, IFPRI, and Concern Worldwide (7)]



through the emission of greenhouse gases such as carbon dioxide and methane, and from changes in land use. Carbon dioxide (CO₂) levels in the atmosphere have increased from about 284 ppm in 1832 to 397 ppm in 2013 (16), and there is a theoretical link between the levels of such “greenhouse” gases in the atmosphere and global warming. Three independent reviews have found strong evidence for human causes for the observed temperature warming mainly caused by the burning of fossil fuels, with smaller contributions from land-use changes (15–18).

Thus, climate change is expected to bring warmer temperatures; changes to rainfall patterns; and increased frequency, and perhaps severity, of extreme weather. By the end of this century, the global mean temperature could be 1.8° to 4.0°C warmer than at the end of the previous century (15). Warming will not be even across the globe and is likely to be greater over land compared with oceans, toward the poles, and in arid regions (15). Recent weather records also show that land surface temperatures may be increasing more slowly than expected from climate models, potentially because of a higher level of absorption of CO₂ by deep oceans (19). Sea-level rises will increase the risk of flooding of agricultural land in coastal regions. Changes in rainfall patterns, particularly over tropical land, are less certain, partly because of the inability of the current models to represent the global hydrological cycle accurately (20). In general, it is expected that the summer Asian monsoon rainfall may increase, while parts of North and southern Africa could become drier (15). How will these regional changes in climate affect food security?

Research Biases

Agriculture is inherently sensitive to climate variability and change, as a result of either natural causes or human activities. Climate change caused by emissions of greenhouse gases is expected to directly influence crop production systems for food, feed, or fodder; to affect livestock health; and to alter the pattern and balance of trade of food and food products. These impacts will vary with the degree of warming and associated changes in rainfall patterns, as well as from one location to another.

Climate change could have a range of direct and indirect effects on all four dimensions of food security. How is the evidence base distributed across the dimensions of food security? We undertook a bibliographic analysis of peer-reviewed journal papers on food security and climate change since the publication of the first Intergovernmental Panel on Climate Change (IPCC) report in 1990 (21). That report was ground-breaking for the climate science that it reviewed, but agriculture was entirely absent. Our analysis shows that a small peak of papers with climate change and food security in the title or abstract were published in the mid-1990s, followed by a lull then a sharp increase in papers published with these terms from 2008 onward.

The distribution of the evidence across the four dimensions of food security is, however, heavily skewed toward food availability within 70% of the publications. Access, utilization, and stability dimensions of food security are represented by only 11.9, 13.9, and 4.2% of the total publications on food security and climate change, respectively.

Why is the evidence based on climate change impacts so unevenly distributed across the four dimensions of food security? There are several possibilities. Research has largely concentrated on the direct effects of climate change, such as those on crop growth and on the distribution of agricultural pests and diseases. Also, studies have understandably focused on areas that can be easily investigated, often through analyzing single-factor changes, and have avoided the com-

plex and multilayered features of food security that require integrations of biophysical, economic, and social factors. Clearly, current knowledge of food security impacts of climate change is dramatically lacking in coverage across all dimensions of food security. Nevertheless, where there is good evidence, what are the broad conclusions?

Food Availability

Rosenzweig and Parry (22) produced the first global assessment of the potential impacts of climate change scenarios on crops. They used numerical crop models of wheat, rice, maize, and soybeans to simulate yields at 112 locations in 18 countries, in the current climate and under climate change using the output of three climate models. These point-based estimates of change

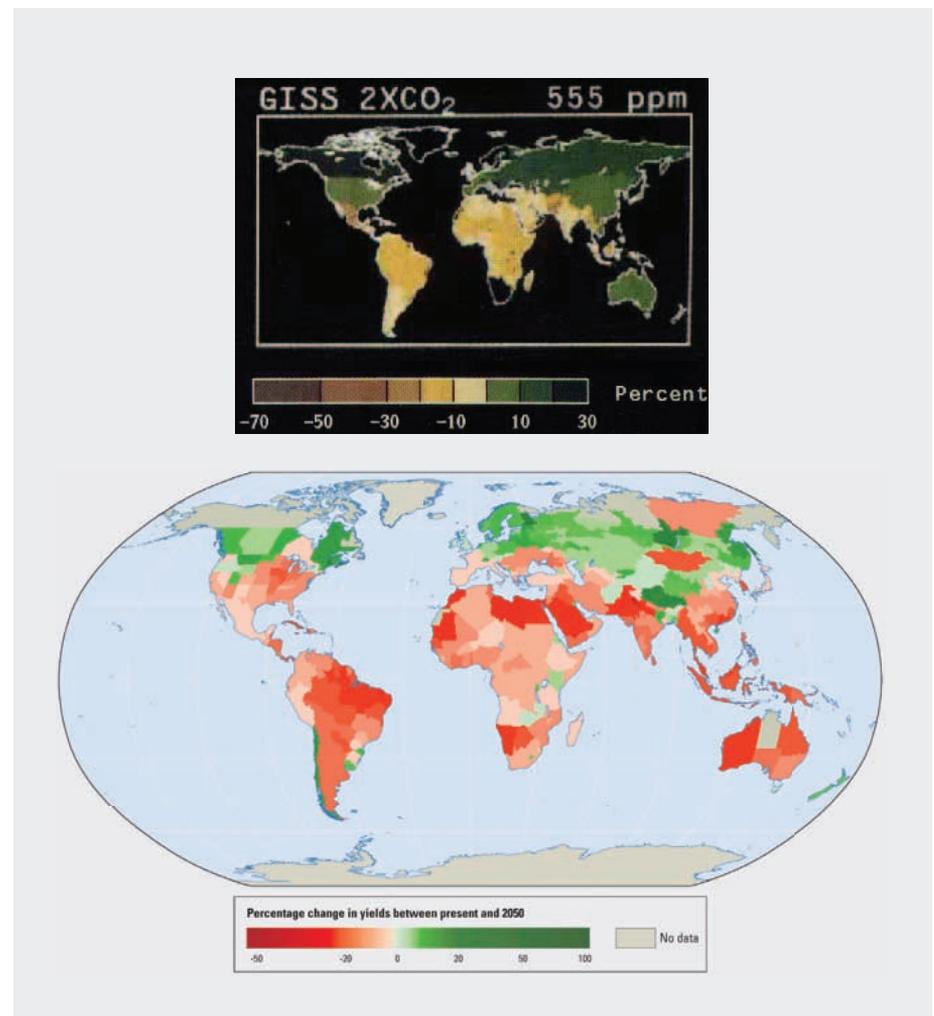


Fig. 2. Global impacts of climate change on crop productivity from simulations published in 1994 and 2010. (Top) The 1994 study (22) used output from the GISS GCM (in this example) with twice the baseline atmospheric CO₂ equivalent concentrations as input to crop models for wheat, maize, soybean, and rice that were run at 112 sites in 18 countries. Crop model outputs were aggregated to a national level using production statistics. **(Bottom)** The 2010 study (27) simulated changes in yields of 11 crops for the year 2050, averaged across three greenhouse emission scenarios and five GCMs. [Reprinted by permission from (top) Macmillan Publishers Ltd. (22); (bottom) World Bank Publishers (27)]

were then scaled-up to country level by using national crop production statistics. Future climate simulations under both present-day and doubled- CO_2 concentrations were used. They found that enhanced concentrations of atmospheric CO_2 increase the productivity of most crops through increasing the rate of leaf photosynthesis and improving the efficiency of water use. However, more recent research has proposed that the CO_2 yield enhancement in crop models is too large compared with observations of crop experiments under field conditions (23). If true, these revised estimates will affect the magnitude of the previous global crop yield changes but not the spatial distribution of impacts. Even if there is some debate on the magnitude of CO_2 effects, higher concentrations of CO_2 in the atmosphere are already having noticeable continental level effects on plant growth in sub-Saharan Africa (24).

The simulations of Rosenzweig and Parry (22) showed that there is a large degree of spatial variation in crop yields across the globe. Both the sign and magnitude of the projected changes in crop yield vary with alternative climate models and from one country to another. In general, yields increased in Northern Europe, but decreased across Africa and South America (22) (Fig. 2). Inevitably, there were methodological weaknesses in this study, including the use of only just over one hundred points to represent global crop production, the absence of any change in the areas suitable for crop production in future climates, limitations on how each of the model points is representative of their surrounding regions, and assumptions about varieties in the crop model parameters themselves. Nevertheless, as the first example of global impacts of climate change on crop production, these simulations are remarkable.

Since 1994, knowledge of the effects of climate on crop plant physiology has improved, the skill of simulation methods for climate change impact studies has increased, and better computing power and data sets to run global simulations have become available. Landmark studies since 1994 include those by Parry and colleagues (25), Cline (26), and, most recently, the World Bank (27) (Fig. 2). Specific projections vary with the climate model scenario used, the simulations methods, and the time scale over which the projections are done. However, the broad-scale pattern of climate change impacts on crop productivity and production has remained consistent across all of these global studies spanning almost 20 years of research. Crop yields are more negatively affected across most tropical areas than at higher latitudes, and impacts become more severe with an increasing degree of climate change. Furthermore, large parts of the world where crop productivity is expected to decline under climate change (Fig. 2) coincide with countries that currently have a high burden of hunger (Fig. 1). We conclude that there is a robust and coherent pattern on a global scale of the impacts of climate change

on crop productivity and, hence, on food availability and that climate change will exacerbate food insecurity in areas that already currently have a high prevalence of hunger and undernutrition.

A recent systematic review of changes in the yields of the major crops grown across Africa and South Asia under climate change found that average crop yields may decline across both regions by 8% by the 2050s (28). Across Africa, yields are predicted to change by -17% (wheat), -5% (maize), -15% (sorghum), and -10% (millet) and, across South Asia, by -16% (maize) and -11% (sorghum) under climate change. No mean change in yield was detected for rice. Knox *et al.* (28) concluded that evidence for the impact of climate change on crop productivity in Africa and South Asia is robust for wheat, maize, sorghum, and millet, and inconclusive, absent, or contradictory for rice, cassava, and sugarcane.

Global-scale climate change impacts at a grid scale of 200 to 250 km can provide useful information on shifts in production zones and perhaps guide the focus of global crop improvement programs seeking to develop better-adapted crop varieties. However, much of the adaptation of agricultural practice to climate change will be driven by decisions at the farm and farm-enterprise scale. These decisions need much finer resolution information than that shown in Fig. 2. At much finer grid scales of 5 to 20 km there are even greater limits to the skill of predictive crop science than at the global scale. Additional uncertainties arise from how the output of global-scale climate models is down-scaled, whether input data (such as crop, soil, topographic, and management information) are available across the domain for crop simulation at this scale, as well as questions as to how skillful the simulation methods are across a fine-scale domain. Recent attempts to harmonize modeling approaches for wheat simulations under climate change found considerable variation in projected impacts among models owing to differences in model structures and parameter values (29). It is not surprising that the sheer complexity of food production systems at a very fine scale is difficult to reproduce in numerical models. However, there is a real need for studies that test how well fine-scale simulations compare with observations in the current climate, as a necessary test of their utility in future climates.

Although the evidence for direct climate change effects on crop productivity is reasonable, important limitations remain for impacts on food availability more broadly. First, models that adequately capture expected climate change effects on crops are only available for the major cereals, groundnut, and some roots and tubers. Impacts on other important crops (such as vegetables, pulses, and locally important, but globally minor, crops) are often inferred based on similar plant characteristics, rather than studied explicitly. Second, changes in grassland productivity and grazing quality and the quality of crops for livestock feed (30) have hardly

been captured, which limits the understanding of climate change–livestock linkages. Last, many crop studies capture the impacts of mean changes in climate, but are less accurate for changes in weather extremes, which can have even more important consequences for crop yields (31).

Food Access

Food access (and utilization) connects to climate change through indirect, but well-known, pathways. Access to food is largely a matter of household and individual-level income and of capabilities and rights. Food access issues have been studied through two types of approaches: top-down by models that attempt to link macro-shocks to household level responses and adaptation outcomes; and by community- and household-level studies that try to assess climate change effects from the bottom up.

The macro-models are often composed of interlinked models—including climate, crop, and economic models. In this approach, outcomes from a climate model feed into the crop model to simulate crop yields under different climate scenarios. The simulated yields are then used to make economic forecasts for the impact of climate change on prices, incomes, trade, and such like. The macro-models can either be constructed following a partial equilibrium approach, i.e., studying the impacts only in one specific sector, such as agriculture, or as general equilibrium models seeking to capture the impacts on the whole economy. The weakness of this approach is that it barely captures climate adaptations. In contrast, micro-level studies are often based on detailed household surveys and usually better account for adaptation by households and communities to climate change.

An important example is the International Food Policy Research Institute (IFPRI) International Model for Policy Analysis of Agricultural Commodities and Trade (IMPACT) model, which connects climate change scenarios with food supply effects and market and price outcomes, and traces the economic consequences of food availability drivers to access and utilization of food, that is, food energy consumption and children's nutritional situation (32, 33). Specific findings are heavily dependent on the assumptions made about future income and population growth but, in general, show clear linkages between economic growth and resilience to climate change (32).

A host of studies is emerging that analyzes what happens to communities and households when they are exposed to climate shocks (34–37). These approaches tend to capture more adaptation capabilities than macro-models, such as asset draw-down, job-switching, migration, social policy responses, and collective action for adaptation and assistance. But it is difficult to appropriately capture with micro-level studies the covariate risks of climate change that cut across broad regions.

Climate change could transform the ability to produce certain products at regional and international levels. If it turns out, for example, that the



geography of biomass production shifts at a global scale (38), this will have production implications for all bio-based products—whether food, feed, fuels, or fiber—and will impinge on food trade flows, with implications for (farm) incomes and access to food (39). Similar changes have been observed in the geography and relative productivity of certain ocean species, such as shifts between anchovy and sardine regimes in the Pacific Ocean (40).

Thus, macro-modeling and micro-level analyses of climate change linkages to food security are complementary. The prices of the basic resources, such as land and water, are formed by long-term expectations (41, 42), and these prices encompass expectations of climate change, such as reevaluation of land with access to water. Structural consequences can emerge, particularly when property rights are lacking and traditional land and water rights are not protected, as is the case in many developing countries with food security problems (43–45); these structural problems lead to erosion of the assets of the poor, as seen during “land grabbing” by external and foreign interests (46).

Food Utilization

Food utilization, to attain nutritional well-being, depends upon water and sanitation and will be affected by any impact of climate change on the health environment. Little research has been done on this dimension of food and nutrition security. Links with drinking water may be obvious, when climate variability stresses clean drinking water availability (47, 48). Hygiene may also be affected by extreme weather events causing flooding or drought in environments where sound sanitation is absent (49–51). In addition, uptake of micronutrients is adversely affected by the prevalence of diarrheal diseases, which in turn is strongly correlated with temperature (52).

Climate change can also impinge on diet quality, and increased costs may result from measures required to avoid food contamination stemming from ecological shifts of pests and diseases of stored crops or food (53, 54). Science and innovation have a role to play here, and in recent years there has been good progress made in improving food utilization through fortification and biofortification (55, 56). Vulnerability to food security shocks needs further research, as do ways to strengthen adaptive capacities under climate change, (57) as public policy responses depend on such insights. For example, appropriate design of programs transferring income to the poor, employment-related transfer programs, and early childhood nutrition actions (58–60) may all need expanding to respond to climate-related volatilities.

New nutritional stresses are emerging, and the most striking example has been the recent “nutrition transition,” i.e., the process by which globalization, urbanization, and changes in lifestyle are linked to excess caloric intake, poor-quality diets, and low physical activity. Together, these factors have led to rapid rises in the inci-

dence of obesity and chronic diseases, even among the poor, in developing countries (61). The nutrition transition will unfold in parallel with climate change in coming decades, but very little research on the potentially reinforcing effects of these phenomena has been done.

Stability of the Food System

The stability of whole food systems may be at risk under climate change, as climate can be an important determinant for future price trends (32), as well as the short-term variability of prices. Since 2007, the world food equation has been at a precariously low level and, consequently, even small shocks on the supply or demand side of the equation will have large impacts on prices, as experienced in 2008 (62). Food security of the poor is strongly affected by staple food prices, as a large part of an impoverished family’s income has to be spent on staple foods.

Climate change is likely to increase food market volatility for both production and supply [see (63) for the supply side]. Food system stability can also be endangered by demand shocks, for instance, when aggressive bioenergy subsidies and quota policies were applied by the political economy (64). These sorts of policy shifts, made in the past decade by the United States and the European Union, have been motivated in part by energy security concerns and partly by climate mitigation objectives (65–67). The resulting destabilization of food markets, which contributed to major food security problems, was therefore partly related to climate change (policy).

The 2008 food crisis stemmed from a combination of a general reduction of agricultural productivity and acute policy failures, exacerbated by export restrictions applied by many countries, a lack of transparency in markets, and poor regulation of financial engagement in food commodity markets (68, 69). A broad set of risks needs to be considered, of which climate change is an increasingly important one, that can ripple out to destabilize food systems, resulting in high and volatile food prices that temporarily limit poor people’s food consumption (70–73), financial and economic shocks that lead to job loss and credit constraints (74), and risks that political disruptions and failed political systems cause food insecurity (75). This complex system of risks can assume a variety of patterns that could potentially collide in catastrophic combinations.

What We Need to Know—Research and Evidence Gaps

Despite a burgeoning literature over the past 5 years or so, much remains unknown about many food security impacts of climate change. Getting better evidence will help to some extent. For example, uncertainties in understanding the underlying science, social science, and economics of climate change impacts will reduce as the evidence base expands with more research. How-

ever, other uncertainties will always remain as they arise from projections of climate change, sources of natural variability in climate, and future pathways of emissions of greenhouse gases.

Four broad priorities for future research emerge from our review: (i) gathering evidence on the effects of climate change impacts on the food access, utilization, and stability dimensions in order to achieve a more holistic understanding of food security; (ii) understanding the indirect impacts of climate change on food security requires more comprehensive analytical approaches and sophisticated modeling, including links to the political economy; (iii) improving projections of regional climate change effects on food security at country level and on smaller scales that are crucial for decision-making for adaptation of food systems; (iv) better integrating of human dimensions of climate change impacts into food security planning—because food systems are ultimately driven by people and their behavioural responses to real and perceived changes in their local climate—that will be central to the adaptation to climate change and actions to address hunger.

What We Know We Know—Messages for Decision-Makers

Decisions still need to be taken by policy-makers and practitioners confronted with the prospect of climate change impacts on food security, despite very real uncertainties in current knowledge and future trends. For those making decisions, we propose, with a fair degree of confidence from the existing evidence, six precepts for the impacts of climate change on food security:

- 1) Climate change impacts on food security will be worst in countries already suffering high levels of hunger and will worsen over time.
- 2) The consequences for global undernutrition and malnutrition of doing nothing in response to climate change are potentially large and will increase over time.
- 3) Food inequalities will increase, from local to global levels, because the degree of climate change and the extent of its effects on people will differ from one part of the world to another, from one community to the next, and between rural and urban areas.
- 4) People and communities who are vulnerable to the effects of extreme weather now will become more vulnerable in the future and less resilient to climate shocks.
- 5) There is a commitment to climate change of 20 to 30 years into the future as a result of past emissions of greenhouse gases that necessitates immediate adaptation actions to address global food insecurity over the next two to three decades.
- 6) Extreme weather events are likely to become more frequent in the future and will increase risks and uncertainties within the global food system.

All of these precepts support the need for considerable investment in adaptation and mit-

igation actions to prevent the impacts of climate change from slowing progress in eradicating global hunger and undernutrition. A wide range of potential adaptation and resilience options exist and more are being developed. These need to address food security in its broadest sense and to be integrated into the development of agriculture worldwide. Building agricultural resilience, or “climate-smart agriculture,” through improvements in technology and management systems is a key part of this, but will not be sufficient on its own to achieve global food security. The whole food system needs to adjust to climate change, with strong attention also to trade, stocks, and to nutrition and social policy options. We need to work toward what could be termed a climate-smart food system that addresses climate change impacts on all dimensions of food security.

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REVIEW

Climate Change and Infectious Diseases: From Evidence to a Predictive Framework

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Scientists have long predicted large-scale responses of infectious diseases to climate change, giving rise to a polarizing debate, especially concerning human pathogens for which socioeconomic drivers and control measures can limit the detection of climate-mediated changes. Climate change has already increased the occurrence of diseases in some natural and agricultural systems, but in many cases, outcomes depend on the form of climate change and details of the host-pathogen system. In this review, we highlight research progress and gaps that have emerged during the past decade and develop a predictive framework that integrates knowledge from ecophysiology and community ecology with modeling approaches. Future work must continue to anticipate and monitor pathogen biodiversity and disease trends in natural ecosystems and identify opportunities to mitigate the impacts of climate-driven disease emergence.

The life cycles and transmission of many infectious agents—including those causing disease in humans, agricultural systems, and free-living animals and plants—are inextricably tied to climate (1, 2). Over the past decade, climate warming has already caused profound and often complex changes in the prevalence or severity of some infectious diseases (Fig. 1) (2–5). For human diseases, vector-control, antimicrobial treatments, and infrastructural changes can dampen or mask climate effects. Wildlife and plant diseases are generally less influenced by these control measures, making the climate signal easier to detect (4). For example, although the effects of climate warming on the dynamics of human malaria are debated, climate warming is consistently shown to increase the intensity and/or latitudinal and altitudinal range of avian malaria in wild birds (6, 7).

Predicting the consequences of climate change for infectious disease severity and distributions remains a persistent challenge surrounded by much controversy, particularly for vector-borne infections of humans [boxes S1 and S2 (8)]. Work using climate-based envelope models has predicted that modest climate-induced range expansions of human malaria in some areas will be offset by range contractions in other locations (9). An alternative approach, based on mechanistic

models of physiological and demographic processes of vectors and pathogens (10), predicts large geographic range expansions of human malaria into higher latitudes (11). Both approaches have their limitations (2), and the challenge remains to accurately capture the contributions of multiple, interacting, and often nonlinear underlying responses of host, pathogen, and vector to climate. This challenge is further exacerbated by variation in the climate responses among host-pathogen systems arising from different life history characteristics and thermal niches (12).

A decade ago, Harvell *et al.* (1) reviewed the potential for infectious diseases to increase with climate warming. Since then, the frequency of studies examining climate-disease interactions has continued to increase (Fig. 2), producing clear evidence that changes in mean temperature or climate variability can alter disease risk. Some of the best examples of climate responses of infectious diseases to date are from ectothermic hosts and from parasites with environmental transmission stages that can persist outside the host (Fig. 1). Indeed, first principles suggest that the rates of replication, development, and transmission of these pathogens should depend more strongly on temperature relative to other host-pathogen interactions. The next challenges require integrating theoretical, observational, and experimental approaches to better predict the direction and magnitude of changes in disease risk. Identifying the contribution of other environmental variables, such as precipitation, humidity, and climate variability remains a challenge (13, 14).

Here, we review the individual, community, and landscape-level mechanisms behind climate-induced changes in infectious disease risk and illustrate how a quantitative, ecophysiological framework can predict the response of different host-pathogen relations to climate warm-

ing. We mainly focus on changes in temperature, which have been more thoroughly explored both empirically and theoretically, relative to other environmental variables. We consider impacts of climate change on human diseases and on pathogens affecting species of conservation or economic concern, including agroecosystems [box S3 (8)]. A crucial need remains for long-term ecological studies that examine the consequences of climate-disease interactions for entire communities and ecosystems, as well as for efforts that couple effective disease forecasting models with mitigation and solutions.

Ecophysiology of Host-Pathogen Interactions

More than a century of research has firmly established that temperature and other climatic variables strongly affect the physiology and demography of free-living and parasitic species [e.g., (15)], with effects on behavior, development, fecundity, and mortality (16). Because these effects can be nonlinear and sometimes conflicting, such as warmer temperatures accelerating invertebrate development but reducing life span, a central challenge has been to identify the net outcomes for fitness (1). For infectious diseases, this challenge is compounded by the interactions between at least two species—a host and a pathogen—and often vectors or intermediate hosts, which make the cumulative influence of climate on disease outcomes elusive [e.g., (17, 18)].

Immune defenses are physiological processes crucial for predicting changes in disease dynamics. Warmer temperatures can increase immune enzyme activity and bacterial resistance for insects, such as the cricket *Gryllus texensis* (19). Positive effects of temperature on parasite growth and replication, however, might outweigh greater immune function of the host. In gorgonian corals, for example, warmer temperatures increase cellular and humoral defenses (20), but because coral pathogens also replicate faster under these conditions, disease outbreaks have coincided with warmer sea temperatures in the Caribbean (Fig. 1) (4, 5). Warm temperatures also can lower host immunity; for example, melanization and phagocytic cell activity in mosquitoes are depressed at higher temperatures (21). In addition, increased climate variability can interfere with host immunity, as illustrated by decreased frog resistance to the chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*) in response to temperature fluctuations (14). Even though *Bd* grows best in culture at cooler temperatures, which suggests that warming should reduce disease, incorporating variability-induced changes in host resistance suggests a more complex relation between climate change and *Bd*-induced amphibian declines (22). These issues are important for predicting the immunological efficiency of ectotherms outside of their typical climate envelope.

One promising approach for predicting how host-pathogen interactions respond to climate

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Fig. 1. Animal-parasite interactions for which field or experimental studies have linked climate change to altered disease risk. (A) Black-legged ticks, *Ixodes scapularis*, vectors of Lyme disease, attached to the ears of a white-footed mouse, *Peromyscus leucopus*, show greater synchrony in larval and nymphal feeding in response to milder climates, leading to more rapid Lyme transmission. (B) Caribbean coral (*Diploria labyrinthiformis*) was affected by loss of symbionts, white plague disease, and ciliate infection during the 2010 warm thermal anomaly in Curaçao. (C) Malformed leopard frog (*Lithobates pipiens*) as a result of infection by the cercarial stage (inset) of the multihost trematode *R. ondatrae*; warming causes nonlinear changes in both host and parasite that lead to marked shifts in the timing of interactions. (D) Infection of monarchs (*D. plexippus*) by the protozoan *O. elektrosirra* (inset) increases in parts of the United States where monarchs breed year-round as a result of the establishment of exotic milkweed species and milder winter climates. (E) Infection risk with *O. gruehneri* (inset shows eggs and larvae) the common abomasal nematode of caribou and reindeer (*R. tarandus*), may be reduced during the hottest part of the Arctic summer as a result of warming, which leads to two annual transmission peaks rather than one (e.g., Fig. 3C). Photo credits (A to E): J. Brunner, E. Weil, D. Herasimtschuk, S. Altizer, P. Davis, S. Kutz.

warming involves infusing epidemiological models with relations derived from the metabolic theory of ecology (MTE). This approach circumvents the need for detailed species-specific development and survival parameters by using established relations between metabolism, ambient temperature, and body size to predict responses to climate warming (23). One breakthrough study (12) used MTE coupled with traditional host-parasite transmission models to examine how changes in seasonal and annual temperature affected the basic reproduction number (R_0) of strongylid nematodes with direct life cycles and transmission stages that are shed into the environment. By casting R_0 in terms of temperature-induced tradeoffs between parasite development and mortality, this approach facilitated both general predictions about how infection patterns change with warming and, when parameterized for *Ostertagia gruehneri*, a nematode of caribou and reindeer (Fig. 1), specific projections that corresponded with the observed temperature dependence of parasite stages. More-

over, this model predicted a shift from one to two peaks in nematode transmission each year under warming conditions (Fig. 3C), a result consistent with field observations (12, 24).

In some cases, ecophysiological approaches must consider multiple host species and parasite developmental stages that could show differential sensitivity to warming. Such differential responses can complicate prediction of net effects, especially for ectothermic hosts with more pronounced responses to temperature. For instance, because both infectivity of a trematode parasite (*Ribeiroia ondatrae*) and defenses of an amphibian host (*Pseudacris regilla*) increase with temperature, maximal pathology (limb malformations) (Fig. 1) occurs at intermediate temperatures (25). Other work showed that the virulence of both a coral fungus (*Aspergillus sydowii*) and protozoan (*Aplanochytrium* sp.) increased with temperature, probably because pathogen development rate continued to increase in a temperature range where coral defenses were less potent (26). Thus, the

ideal approach will be an iterative one that combines metabolic and epidemiological modeling to predict general responses and to identify knowledge gaps, followed by application of models to specific host-pathogen interactions.

Community Ecology, Biodiversity, and Climate Change

Host-pathogen interactions are embedded in diverse communities, with climate change likely leading to the loss of some host-pathogen interactions and the gain of novel species pairings. In some cases, pathogen extinction and the loss of endemic parasites could follow from climate change, potentially reducing disease or conversely releasing more pathogenic organisms from competition. In other cases, multiple pathogens can put entire host communities at risk of extinction. Although ecosystems of low biodiversity, such as occur in polar regions, can be particularly sensitive to emerging parasitic diseases (27), most knowledge of community-wide responses stems from tropical marine systems. For example, the wider Caribbean region is a “disease hot spot” characterized by the rapid, warming-induced emergence of multiple new pathogens that have caused precipitous coral declines with ecosystem-wide repercussions (28, 29). Impacts of climate-induced changes in disease can be especially large

when the host is a dominant or keystone species. For example, near extinction of the once-dominant, herbivorous abalone (genus *Haliotis*) by warming-driven rickettsial disease caused pervasive community shifts across multiple trophic levels (5). Similarly, seagrass (*Zostera marina*) declines caused by infection with the protist *Labyrinthula zosterae*, which correlates positively with warming, have degraded nursery habitats for fish and migratory waterfowl and caused the extinction of the eelgrass limpet (30).

Microbial communities, which are often part of the extended phenotype of host defenses, are also likely to respond to climate changes. For instance, warming sea-surface temperatures in coral reefs can inhibit the growth of antibiotic-producing bacteria, sometimes causing microbial communities to shift from mutualistic to pathogenic (31). In agroecosystems, higher temperatures can suppress entomopathogenic fungi and antibiotic production by bacterial mutualists in plants (32). Warming also underlies bacterial shifts from endosymbiotic



to lytic within host amoebas that live in human nasal passages, increasing the potential risk of respiratory disease (33). Thus, effects of warmer temperatures on the diversity and function of commensal or mutualist microbes could promote pathogen growth and pest outbreaks.

From a broader perspective, biodiversity loss is a well-established consequence of climate change (16, 34) and can have its own impact on infectious diseases. For many diseases of humans, wildlife, and plants, biodiversity loss at local or regional scales can increase rates of pathogen transmission (35–37). This pattern can result from several mechanisms, including the loss of the dilution effect (36). For example, lower parasite diversity could allow more pathogenic species to proliferate when endemic and competing parasites are lost from a system (36). Climate warming can also weaken biotic regulation of disease vectors by inhibiting their predators (38) and competitors (39). Interactions between biodiversity and infectious disease underscore the need to put climate-disease interactions into the broader context of other forms of global change, such as land-use change and habitat loss, when extending predictions from focused host-pathogen interactions to larger spatial and taxonomic scales.

Shifts in Behavior, Movement, and Phenology of Hosts and Parasites

Changes in climate are already affecting the phenology of interactions between plants and pollinators, predators and prey, and plants and herbivores (16). Climate-induced shifts in phenology and species movements (40) will likely affect disease dynamics. Many species are already moving toward higher elevations or latitudes (41), and an open question is whether these shifts could disrupt established interactions or bring novel groups of hosts and pathogens into contact (42). For instance, the range expansion of the Asian tiger mosquito (Aedes albopictus) across Europe and the Americas has created the potential for novel viral diseases such as Chikungunya to invade (10); this pathogen is already expanding in geographic range, and a recent outbreak in Europe emphasizes the need for surveillance and preparedness. Along eastern North America, warming sea temperatures and changes in host resistance facilitated a northward shift of two oyster diseases into previously unexposed populations (5).

Migratory species in particular can be sensitive to climate change (41), with the routes and timing of some species' migrations already shifting with climate warming (16). Long-distance migrations can lower parasite transmission by allowing hosts to escape pathogens that accumulate in the environment or by strenuous journeys that cull sick animals (43). In some cases, milder winters can allow previously migratory host populations to persist year-round in temperate regions (44); this residency fosters the build-up of environmental transmission stages, and mild

winters further enhance parasite over-winter survival (2). A case study of monarch butterflies (Danaus plexippus) and the protozoan parasite Ophryocystis elektroscirrha (Fig. 1) provides support for climate-warming shifts in migration and disease. Monarchs typically leave their northern breeding grounds in early fall and fly to Mexican wintering sites. Milder winters, combined with increased planting of exotic host plants, now allow monarch populations to breed year-round in parts of the United States (45). Relative to migratory monarchs, winter-breeding monarchs suffer from higher rates of infection (43). Similarly, migration is considered an important parasite avoidance strategy for barren-ground caribou (24), but the loss of sea ice with climate warming will likely inhibit migrations and prevent them from seasonally escaping parasites (46). Thus, diminishing migration behaviors among animals that use seasonal habitats can increase the transmission of infectious diseases.

Changes in the timing of vector life stages and feeding behavior can also arise from interactions between climate and photoperiod. For several tick-borne infections (Fig. 1), pathogens are sequentially transmitted from infected vertebrate hosts to naïve larval tick vectors, and from infected nymphal ticks to naïve vertebrate hosts. Asynchrony in the seasonal activity of larval and nymphal ticks can delay transmission and select for less virulent strains of the Lyme bacterium Borrelia burgdorferi (47), whereas synchrony allows for more rapid trans-

mission and the persistence of virulent strains. In the case of tick-borne encephalitis (TBE), viral transmission occurs directly between co-feeding ticks; thus, viral maintenance requires synchronous larval and nymphal feeding (48). Because synchrony of larval and nymphal ticks characterizes milder winter climates, climate change could increase tick synchrony and the transmission and virulence of several tick-borne infections.

Changes in the timing of shedding or development of environmental transmission stages could result from climate warming. Some parasites could experience earlier hatching, exposure to hosts earlier in the season, and encounters with earlier (and often more sensitive) life stages of hosts. For example, a long-term data set of lake plankton showed that warming shifted fungal prevalence patterns in diatom hosts from acute epidemics to chronic persistence, in part because of faster transmission and more widespread host population suppression under warmer temperatures (49). In contrast, Brown and Rohani (50) argued for the opposite outcome with respect to avian influenza (AI) in reservoir bird hosts. Climate-driven mismatch in the timing of bird migration and their prey resources (e.g., horseshoe crab eggs) amplified variability in epidemiological outcomes: Although mismatch increased the likelihood of AI extinction, infection prevalence and spillover potential both increased in cases where the virus persisted.

Plasticity in parasite traits could allow parasites with environmental transmission stages to

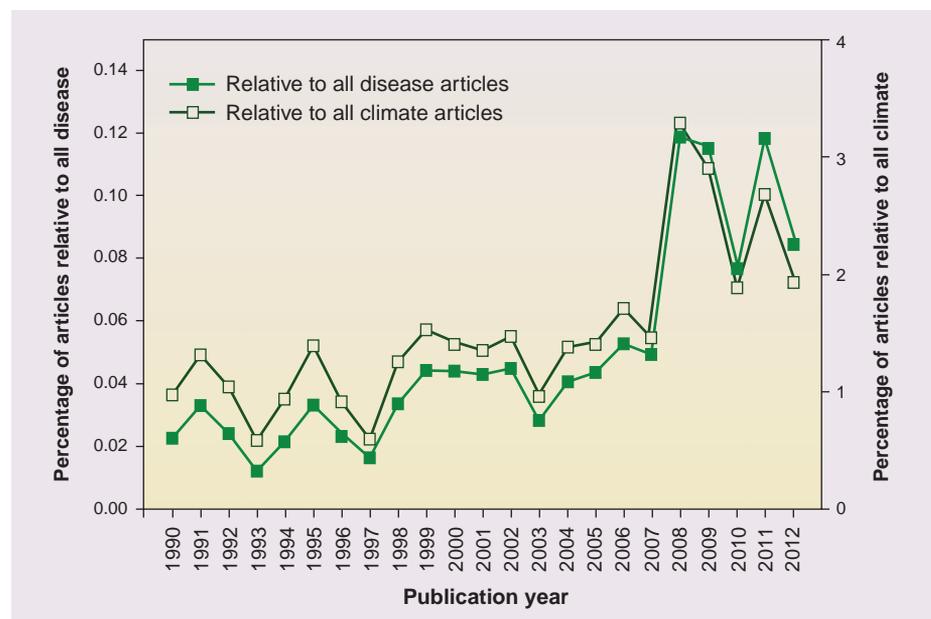


Fig. 2. Rising interest in climate-disease interactions. Research focused on associations between infectious disease and climate change has increased steadily over the past 20 years. After correcting for total research interest in climate change (open symbols) or infectious disease (closed symbols), the frequency of papers referencing a climate-disease link in the title has nearly doubled over this period, based on long-term publication trends following a Web of Science search of article titles (1990 to 2012). Search criteria and statistical analyses are provided in the supplementary materials, and the total number of climate change-infectious disease papers identified by our search criteria ranged from 5 to 117 publications per year.

respond more rapidly to climate warming. For example, arrested development (hypobiosis) of the nematode *O. gruehneri* within its caribou

host is a plastic trait more commonly expressed in areas with harsher winters as compared with milder climates (51). This arrested state prevents

wasted reproductive effort for the parasites, because eggs produced in late summer in colder regions are unlikely to develop to infective-stage larvae by fall. Ultimately, plasticity in life history traits could speed parasite responses to changing environments and allow parasites to deal with climate instabilities (e.g., a series of severe winters interspersed by mild), relative to the case where selection must act on genetically variable traits (52). For example, if climate warming extends the transmission season for *O. gruehneri* on tundra, a rapid decrease in the frequency of nematode hypobiosis could shorten the life cycle and increase infection rates.

Consequences for Conservation and Human Health

Climate change is already contributing to species extinctions, both directly and through interactions with infectious disease (53). Roughly one-third of all coral species and the sustainability of coral reef ecosystems are threatened by human activities, including climate warming and infectious diseases (5). In contrast to tropical marine systems, the Arctic is a less diverse and minimally redundant system that is warming at least twice as fast as the global average (54) and simultaneously experiencing drastic landscape changes from an expanding human footprint. Altered transmission dynamics of parasites, poleward range expansion of hosts and parasites, and disease emergence coincident with climate warming or extremes have all been reported in the Arctic (27, 55). Together, these phenomena are altering host-parasite dynamics and causing endemic Arctic species—unable to compete or adapt rapidly enough—to decline (56). Changes in wildlife health can also compromise the livelihoods and health of indigenous people who depend on wildlife for food and cultural activities (57).

In humans, exposure to diarrheal diseases has been linked to warmer temperatures and heavy rainfall (58). Human infections of cholera, typically acquired through ingestion of contaminated water (in developing countries) or undercooked seafood (in the developed world), affect millions of people annually with a high case-fatality rate. Coastal *Vibrio* infections are associated with zooplankton blooms, warmer water, and severe storms (3). For example, in the Baltic Sea, long-term warming and temperature anomalies have been linked to increased disease from *Vibrio vulnificus*, which was first reported in 1994 along the German coast after an unusually warm summer (3). Long-term sea surface warming can increase the geographic range, concentration, and seasonal duration of *Vibrio* infections, as seen in coastal Chile, Israel, and the U.S. Pacific Northwest. Modeling approaches indicate that *Vibrio* illnesses from the Baltic region could increase nearly twofold for every 1°C increase in annual maximum water temperature (3).

Human mosquito-borne diseases, such as malaria and dengue fever, are frequently proposed

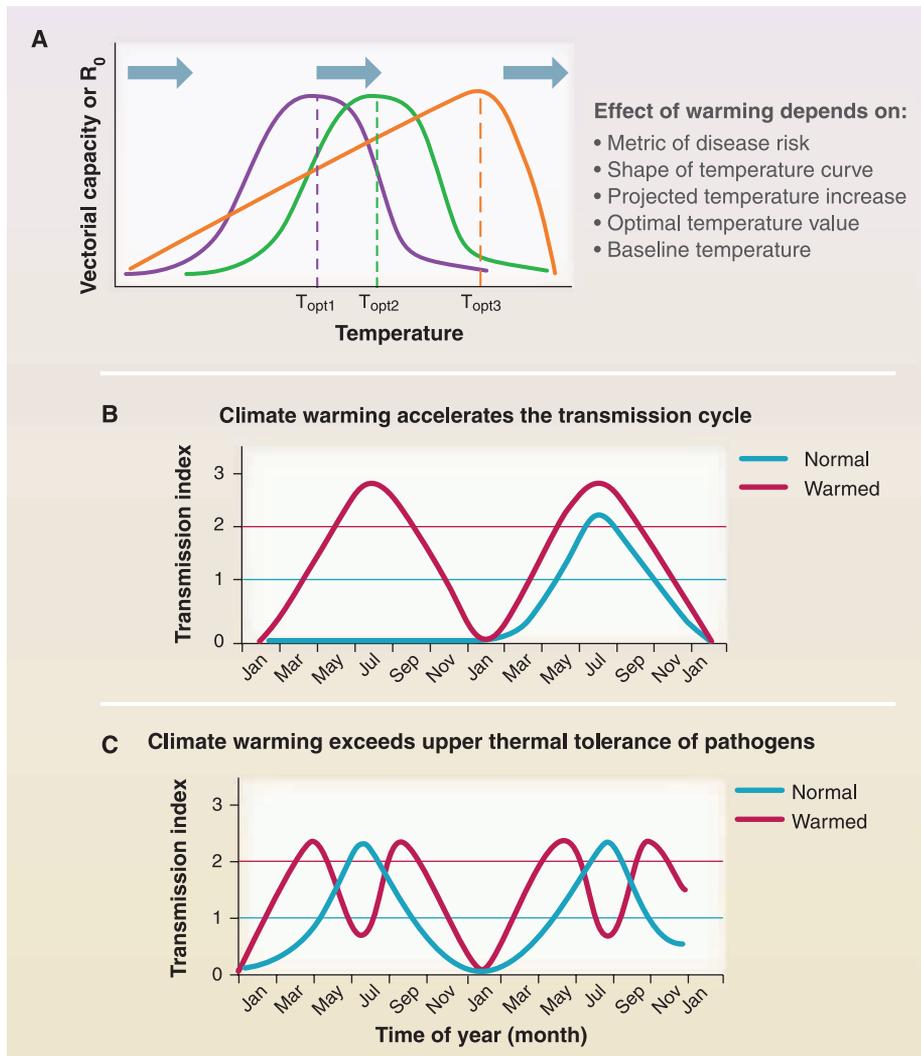


Fig. 3. Theoretical underpinnings and categorization of disease responses to climate change. Pathogen responses to climate change depend on thermal tolerance relative to current and projected conditions across an annual cycle. **(A)** Gaussian curves relating temperature to a metric of disease risk suggest symmetrical temperature zones over which warming will increase and decrease transmission, whereas left-skewing [a common response for many terrestrial ectotherms, including arthropod vectors (74)] indicates greater potential for pathogen transmission to increase with warming [box S2 (8)]. Bold arrows represent geographic gradients that span cool, warm, and hot mean temperatures, which indicate that the net effect of warming (at point of arrows) depends on whether temperatures grow to exceed the optimum temperature (T_{opt}) for disease transmission. Projected changes in disease will further depend on the starting temperature relative to T_{opt} , the magnitude of warming, measurement error, adaptation, and acclimation. **(B)** Pathogens at their northern or altitudinal limits might show range expansion and nonlinear shifts in their life cycle in response to warmer temperatures (red) relative to baseline (blue). For example, a shift from 2- to 1-year cycles of transmission has occurred for the muskox lungworm (27). This outcome could generate sporadic disease emergence in a naïve population (if extremes in temperature allow only occasional invasion and/or establishment), or could gradually increase prevalence and establishment. **(C)** At the low-latitude or low-altitude extent of a pathogen's range, where temperature increases could exceed the pathogen's thermal optimum, transmission might be reduced, or we might see the emergence of a bimodal pattern whereby R_0 peaks both early and late in the season, but decreases during the midsummer [as in the case of the arctic *O. gruehneri*-reindeer example (12)]. In **(B)** and **(C)**, the lower blue line represents $R_0 = 1$, above which the pathogen can increase; values above the pink line represent severe disease problems owing to a higher peak of R_0 and a greater duration of time during which $R_0 > 1$.



as cases where vector and disease expansion into the temperate zone could follow from climate warming (59). However, some researchers have argued that ranges will shift with warming, rather than expand, and that the best predictors of infection risk are economic and social factors, especially poverty (17, 60). Controversy has also arisen over which climatic variables are most important in delimiting the distributions of these diseases [boxes S1 and S2 (8)]. Detecting impacts of climate change on human vector-borne diseases remains difficult, in part, because active mitigations, such as vector-control, antimicrobials, and improved infrastructure can complicate detection of a climate signal. Several unresolved issues include identifying conditions under which climate warming will cause range expansions versus contractions, understanding the impact of increasing variability in precipitation, and determining the additional economic costs associated with increased disease risk caused by warming.

Ultimately, the societal implications of climate-driven shifts in diseases of humans, crops, and natural systems will demand solutions and mitigation, including early-warning programs. Recently, a forecasting system linking global coupled ocean-atmosphere climate models to malaria risk in Botswana allowed anomalously high risk to be predicted and anticipatory mitigations to be initiated (61). Forecasting is well-established in crop disease management and leads to improved timing of pesticide application and deployment of planting strategies to lower disease risk [box S3 (8)]. Modeling efforts to better predict crop loss events are also tied to improved insurance returns against losses (2). Similarly, accurate forecasting programs for coral bleaching have become a mainstay of marine climate resilience programs (62) and are leading to the development of coral disease-forecasting algorithms (63). Appropriate management actions under outbreak conditions include reef closures to reduce stress and transmission, culling of diseased parts of some colonies, and increased surveillance (64). In the ocean, efforts are also under way to increase the resilience of marine ecosystems to disease, including developing no-fishing zones and reducing land-based pollution that can introduce new pathogens (5).

Outlook and Future Challenges

Climate change will continue to limit the transmission of some pathogens and create opportunities for others. To improve predictions and responses we need to deepen our understanding of mechanistic factors. Although the initial climatic drivers to be explored should be temperature variables (both mean and variability), because the data are available and we understand the mechanisms at work, future work must concurrently explore the effects of precipitation, relative humidity, and extreme events. In particular, models are needed that combine the principles of ecophysiology and MTE (23) with epidemiological response variables, such

as R_0 or outbreak size, and that are designed to accommodate distinct pathogen types (e.g., vector-borne, directly transmitted, or complex life cycle) and host types (ectotherm versus endotherm) (12). These models should be applied, by using climate-change projections, to evaluate how broad classes of pathogens might respond to climate change. Building from this foundation, the next step is to extend such general models to specific pathogens of concern for human health, food supply, or wildlife conservation, which will require empirical parameterization, with attention to the on-the-ground conditions. Modeling efforts should be integrated with experiments to test model predictions under realistic conditions, and with retrospective studies to detect the “fingerprint” of climate-induced changes in infection.

Scientists still know relatively little about the conditions under which evolution will shape host and pathogen responses to climate change. Although evolutionary change in response to climate warming has been reported for some free-living animals and plants, the evidence remains limited (52). Even less is known about how climate change will drive host-pathogen evolution. Corals have multiple levels of adaptation to intense selection by thermal stress that could also affect resistance to pathogens, including symbiont shuffling of both algae and bacteria, and natural selection against thermally intolerant individuals (65). In oysters (*Crassostrea virginica*), warming might have contributed to increased resistance to the protozoan multinucleated sphere X (MSX) disease (66), but climate variability might also slow the evolution of oyster resistance (67). In cases where increased rates of transmission follow from warming, selection could favor higher pathogen virulence, although examples are now unknown.

A persistent challenge involves the ability to detect changes in disease risk with climate across different systems. In the oceans, for example, impacts of disease on sessile hosts like corals, abalones, and oysters are readily apparent, and for terrestrial systems, clear impacts are seen for plant diseases and some wildlife-helminth interactions. But for highly mobile species and many human diseases, detecting signals of climate change remains problematic. For these less tractable systems, long-term ecological studies that examine the past distributions of pathogens, important hosts, and severity of diseases are indispensable. Permanent repositories of intact physical specimens, as well as their DNA, can provide records of diversity that will be critical resources as new methodologies become available (68, 69). Moreover, new technologies can detect variability in physiological processes and gene expression and can improve climate projections from global circulation models. Sophisticated experimental designs conducted under appropriate ranges of environmental conditions and retrospective studies to identify past climatic effects on disease (5, 70) will help advance predictive power.

An additional key challenge is predicting the impacts of climate-disease interactions for human societies and gauging how these compare with other components of climate change, such as the loss of arable land. By affecting food yields and nutrition, water quality and quantity, social disorder, population displacement, and conflict, past climate changes have long influenced the burden of infectious disease in many human societies (71, 72). Predicting the regions where humans and natural systems are most vulnerable to pressures from infectious disease and how these pressures will translate to changes in global health and security constitute critical research priorities (73). Building a mechanistic understanding of climate-disease interactions will allow public health interventions to be proactive and will facilitate effective responses to new or expanding health threats. Surveillance programs capable of detecting pathogen or disease emergence are essential and, in many instances, predicting and detecting local-scale impacts might be more important than predicting global-scale changes. To this end, the value of engaging local communities in disease surveillance is increasingly recognized, with the goal of advancing science on climate-disease linkages for practical solutions to protecting human and wildlife health.

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Supplementary Materials

www.sciencemag.org/cgi/content/full/341/6145/514/DC1

Materials and Methods

Supplementary Text

Fig. S1

Boxes S2 to S3

References (75–95)

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REVIEW

Ecological Consequences of Sea-Ice Decline

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After a decade with nine of the lowest arctic sea-ice minima on record, including the historically low minimum in 2012, we synthesize recent developments in the study of ecological responses to sea-ice decline. Sea-ice loss emerges as an important driver of marine and terrestrial ecological dynamics, influencing productivity, species interactions, population mixing, gene flow, and pathogen and disease transmission. Major challenges in the near future include assigning clearer attribution to sea ice as a primary driver of such dynamics, especially in terrestrial systems, and addressing pressures arising from human use of arctic coastal and near-shore areas as sea ice diminishes.

As one of Earth's major biomes, sea ice not only comprises unique ecosystems in, on, and under the ice itself but also strongly influences patterns and processes in adjacent terrestrial ecosystems (1, 2) (Fig. 1). Sea ice harbors an array of microorganisms, provides critical habitat for vertebrates, and influences terrestrial productivity and diversity in the Arctic, where 80% of low-lying tundra lies within 100 km of seasonally ice-covered ocean (3–5). Ice-loss-driven amplification of arctic warming is a potentially important driver of ecological dynamics in the region, where seasonal temperature limitation is an important constraint on productivity (6). Here, we synthesize recent developments in the study of ecological

responses to arctic sea-ice decline and highlight the importance of sea-ice loss as a driver of ecological dynamics in both marine and terrestrial systems.

Record of Recent Sea-Ice Loss

One of the most conspicuous consequences of recent anthropogenic warming has been declining annual minimum extent of arctic sea ice (7). Over the past several decades, the Arctic has warmed at twice the global rate, with sea-ice loss accelerating (8) (Fig. 2A), especially along the coasts of Russia, Alaska, and the Canadian Archipelago (Fig. 2B). The sea ice's annual minimum reached a record low in 2012. Arctic sea-ice loss has exceeded most model pro-

jections (9) and is unprecedented in the past 1.5 millennia (10).

Sea-ice loss is most commonly discussed as an indicator of arctic warming (11), but it is also a major factor in amplification of warming in the Arctic through feedback deriving from declining surface albedo (6). In 2007, the year of second-lowest arctic sea-ice extent on record, sea ice loss accounted for a large portion of warming over land north of 60° (12). Further, much of arctic near-surface warming over the past three decades is attributable to declining sea ice concentration (13), and land-surface warming is linked to summer sea-ice loss in global climate models (14).

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Supplementary Materials for
**Climate Change and Infectious Diseases: From Evidence to a Predictive
Framework**

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Fig. S1
Full References

Materials and Methods

TEMPORAL TRENDS IN DISEASE-CLIMATE RESEARCH

To evaluate long-term publication trends for climate-driven effects on infectious diseases (Fig. 2, Main Text), we conducted a Web of Science search of article titles (1990 to 2012) on 5 June 2013. We focused on articles published during or after 1990 to help standardize the search [i.e., relatively few references were published on the topic prior to this year (75)]. We included all document types (rather than original research articles only) because preliminary searches revealed that several relevant articles from recent special issues (e.g., Ecology 2009) were classified as ‘editorial material.’ Our approach involved first performing separate searches for climate change and for studies of disease (primarily infectious disease and parasitism, see search strings below) and then combining these searches to identify articles included in both. To adjust for long-term changes in research effort, we divided the number of articles on climate change and disease published each year by either the total number of climate change-related articles or the total number of disease-related articles [see (65, 76)]. Effectively, this allowed us to examine patterns in publication on climate-disease articles normalized to research effort on either climate change or disease work generally (see Fig. 2, Main Text). To evaluate whether temporal trends were significant, we used generalized additive autoregressive models followed by AIC value comparisons to assess whether a smoothing term and/or autoregressive and moving average terms provided a better fit to the data relative to simple linear models.

The literature search yielded 67,714 articles on climate change, 2.1 million articles on infectious disease, and 1,047 articles that appeared in both searches. The proportion of disease-climate articles increased over time (see Fig. 2), regardless of which denominator was used. Based on model selection, the effect of year on the proportion of climate-disease articles published (relative to all climate-change articles) was positive and linear (Relative to all climate-change articles, GLM, $\text{year} = 0.073 \pm 0.015$, $t = 4.83$, $P < 0.0001$; Relative to all disease articles, GLM, $\text{year} = 0.0038 \pm 0.00061$, $t = 6.23$, $P < 0.00001$). There was no support for inclusion a smoothing term, autoregressive term, or moving average (i.e., $\Delta\text{AIC} > 2$). Spikes in research activity in 2008 and 2009 were associated with journal special issues on the topic of climate change and disease in *Parasitology Research* and *Ecology*, respectively.

Search string for climate articles included [TI = (((climat* or temperature*) and (change or shift* or disrupt* or anomal* or variation or variability or warm*)) or (global and warming) or (extreme and (event* or drought* or flood* or temperature*)) or (el and nino) or ENSO or (la and nina))]. Search terms for disease included [TI = (disease* or pathog* or infect* or prevalence or parasit* or bacteri* or virus* or viral or fung* or myco* or nematod* or trematod* or cestod* or ectoparasit* or acanthoceph* or protist* or protozoa* or (mass and mortalit*) or dieoff* or epidem* or epizoot* or helminth* or chytrid* or myxozoa* or oomycet* or vibrio* or microsporid* or HABs*)]. Modified from Hoverman et al. (77).

Supplementary Text

BOX S1. HUMAN VECTOR-BORNE DISEASES: CLIMATIC AND NONCLIMATIC DRIVERS, TREATMENT, AND CONTROL

Warming-driven increases in vector and pathogen development coupled with greater vector-biting rates under warmer temperatures create the potential for increased transmission of human vector-borne diseases such as malaria and dengue (but see Box S2 for important nonlinearities). However, this potential might not be realized in areas where economic conditions support adequate vector control, surveillance, health care, housing, or water management, leading some researchers to consider climatic factors relatively unimportant in predicting future human health risks (78, 79). Only recently have models simultaneously addressed both climate-driven and human-driven forces operating on mosquito-borne diseases [e.g., (79)]. Beguin et al. (81) used a global, statistical model to predict the effects of climate change and socioeconomic development on future malaria distribution. With no climate change and a 3-fold projected increase in per capita gross domestic product [pcGDP], the number of people living in at-risk areas is predicted to decline from 2.3 to 1.74 billion by 2050. With projected changes in both pcGDP and climate, however, 1.95 billion are predicted to be at risk – or an additional 210 million people due to climate change (Fig. S1). This estimate will further depend on downward-adjusted projections in pcGDP, which could be an important indirect effect of climate change (82-84). Such results highlight the need for identifying the contributions of climate-mediated effects on disease, which

are likely widespread but occur alongside numerous other forms of global change that must be concurrently understood to both detect climate signals and effectively manage disease into the future.

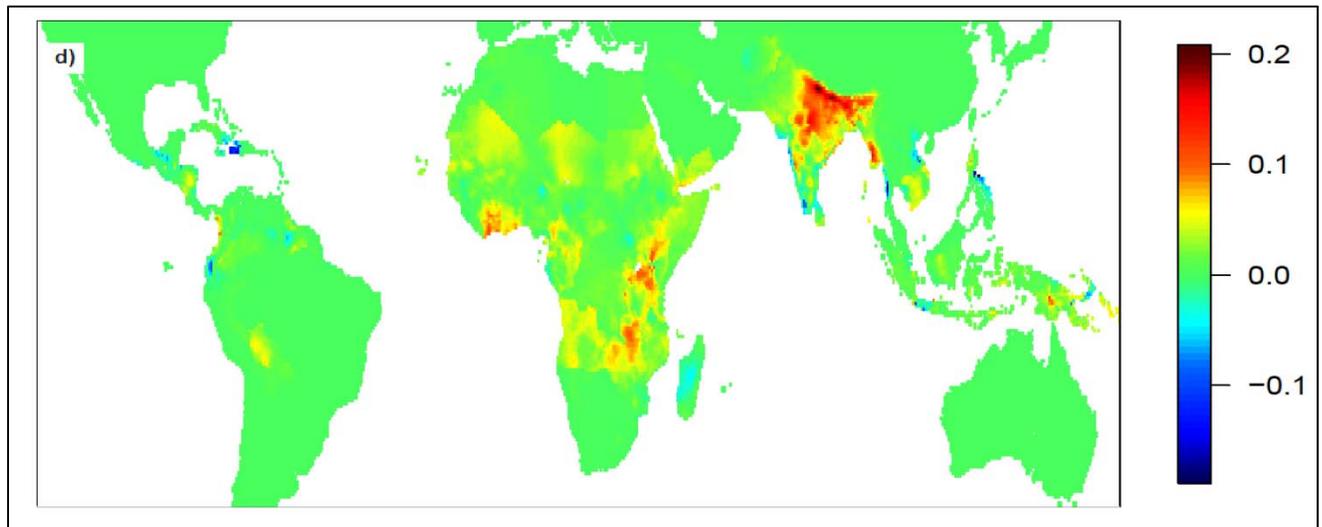


Fig S1. Projected change in global human malaria risk attributable to climate change by 2050 (A1B Scenario, expected to increase the risk of malaria transmission), after also accounting for a projected increase in per capita gross domestic product (expected to strongly decrease transmission). Areas depicted in warmer colors reflect increases in modeled transmission probability. Reprinted with permission from (81).

BOX S2. CLIMATE CHANGE AND THE ECOPHYSIOLOGY OF VECTORS AND THEIR PATHOGENS

Process-based models of climate-change impacts on vector-borne diseases rely on curves relating temperature to vector (and pathogen) vital rates, such as survival, development time, fecundity, and biting rate. To predict how warming affects disease risk, researchers must devise models that link heterogeneous vital-rate curves to an aggregate measure of risk, such as the force of infection, environmental inoculation rate (EIR, number of infected mosquitoes per person), or R_0 (Fig. 3, Main Text). Subsequent increases in complexity, such as incorporating other climatic

variables [e.g., relative humidity, precipitation, and daily or longer-term temperature variability (85-87)], pathogen/vector acclimation and evolution (87), or extrinsic factors such as host immunity and pathogen diversity (89), will amplify this challenge, but doing so is probably essential to achieve realistic predictions. For instance, different risk metrics and model structures have led to predicted optimal temperatures for malaria risk between 25°C and 33°C depending on whether temperature curves are bell-shaped (90) or left-skewed (91, 92). Thus, empirically validated measures of host and pathogen thermal performance curves – including accurate estimates of the temperatures actually experienced by organisms (93) and the degree of local adaptation – are essential in projecting whether local or regional warming will increase or decrease disease risk (Fig. 3) (80, 90). Such information would also shed light on the relative importance of climatic variables such as T_{min} , T_{mean} , and extreme weather events, the effects of which remain controversial.

BOX S3: PLANT DISEASES, AGROECOSYSTEMS AND CLIMATE CHANGE

The host-pathogen systems with the clearest identified links to weather and climate are agroecosystems (72). Climate factors such as temperature and rainfall can affect both the virulence and transmission of crop diseases. The influence of climate is perhaps best understood for rust fungal pathogens, for which short-term forecasting algorithms have been developed. Warming or increased rainfall can increase the probability of outbreaks, and forecasting algorithms allow farmers to apply antifungal agents preemptively. The effects of climate extremes can also extend into a subsequent year; for example, increases in pathogen inoculum load remaining at the end of a season, which tends to occur following warmer winters, can amplify disease severity the following spring (2). Extreme weather events have also been linked to outbreaks of fungal and oomycete pathogens that can cause substantial crop losses (e.g., *Phytophthora drechsleri* f.sp. *cajani* blight in pigeon pea and dry root rot caused by *Rhizoctonia bataticola* in chickpea). Temperature increases associated with the 1997 El Niño in Peru increased the abundance and severity of many agricultural pests and pathogens, including the bud midge (*Prodiplosis longifila*), the potato tuber fly (*Phthorimaea operculella*) and the white fly (*Bemisia tabaci*), ultimately requiring extreme doses of pesticides to control (94, as cited in 2). Agroecosystems also provide a long-term perspective on the relationship between climate and

disease. In a historical evaluation of climate-change effects on late blight trends in Finland between 1933 and 2002, the risk of potato late blight outbreaks was 17-fold higher during the warm period between 1998 and 2002 relative to earlier, comparatively cooler periods, with epidemics initiating 2–4 weeks earlier than observed historically (95). Future climate projections further suggest that, in some regions, agricultural pathogens will be favored in a warming world with important consequences for crop production. In Northern Germany, for instance, oil seed rape fungal pathogens such as *Alternaria brassicae*, *Sclerotinia sclerotiorum*, and *Verticillium longisporum* are predicted to be favored by warmer average temperatures, particularly when taking a long-term (2071–2100) view (96).

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Supplementary Materials

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REVIEW

Ecological Consequences of Sea-Ice Decline

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After a decade with nine of the lowest arctic sea-ice minima on record, including the historically low minimum in 2012, we synthesize recent developments in the study of ecological responses to sea-ice decline. Sea-ice loss emerges as an important driver of marine and terrestrial ecological dynamics, influencing productivity, species interactions, population mixing, gene flow, and pathogen and disease transmission. Major challenges in the near future include assigning clearer attribution to sea ice as a primary driver of such dynamics, especially in terrestrial systems, and addressing pressures arising from human use of arctic coastal and near-shore areas as sea ice diminishes.

As one of Earth's major biomes, sea ice not only comprises unique ecosystems in, on, and under the ice itself but also strongly influences patterns and processes in adjacent terrestrial ecosystems (1, 2) (Fig. 1). Sea ice harbors an array of microorganisms, provides critical habitat for vertebrates, and influences terrestrial productivity and diversity in the Arctic, where 80% of low-lying tundra lies within 100 km of seasonally ice-covered ocean (3–5). Ice-loss-driven amplification of arctic warming is a potentially important driver of ecological dynamics in the region, where seasonal temperature limitation is an important constraint on productivity (6). Here, we synthesize recent developments in the study of ecological

responses to arctic sea-ice decline and highlight the importance of sea-ice loss as a driver of ecological dynamics in both marine and terrestrial systems.

Record of Recent Sea-Ice Loss

One of the most conspicuous consequences of recent anthropogenic warming has been declining annual minimum extent of arctic sea ice (7). Over the past several decades, the Arctic has warmed at twice the global rate, with sea-ice loss accelerating (8) (Fig. 2A), especially along the coasts of Russia, Alaska, and the Canadian Archipelago (Fig. 2B). The sea ice's annual minimum reached a record low in 2012. Arctic sea-ice loss has exceeded most model pro-

jections (9) and is unprecedented in the past 1.5 millennia (10).

Sea-ice loss is most commonly discussed as an indicator of arctic warming (11), but it is also a major factor in amplification of warming in the Arctic through feedback deriving from declining surface albedo (6). In 2007, the year of second-lowest arctic sea-ice extent on record, sea ice loss accounted for a large portion of warming over land north of 60° (12). Further, much of arctic near-surface warming over the past three decades is attributable to declining sea ice concentration (13), and land-surface warming is linked to summer sea-ice loss in global climate models (14).

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Direct Effects of Sea-Ice Loss

Primary producers dependent upon sea ice as their habitat underpin the entire marine food web of the Arctic (Fig. 1A). The loss of over 2 million km² of arctic sea ice since the end of the last century (Fig. 2A) (10) represents a stunning loss of habitat for sea-ice algae and sub-ice phytoplankton, which together account for 57% of the total annual primary production in the Arctic Ocean (15). The seasonal timing of the ice algae bloom, driven by light penetration through thinning sea ice, is critical to the successful reproduction of zooplanktonic copepod grazers, and the timing of the subsequent phytoplankton bloom as the ice edge retreats is critical to the growth and survival of copepod offspring (15). These two annual pulses of productivity, including the release of organic material from seasonally melting ice, fuel the arctic marine food web (2).

Disruption of the seasonality of the ice algal and phytoplankton blooms by ice thinning, accelerated melt timing, and an increase in the length of the annual melt season by 20 days over the past three decades (16) has created mismatches for the timing of zooplankton production, with consequences for higher consumers (17, 18). Earlier seasonal sea-ice melt and earlier phytoplankton blooms may shorten the length of the annual window of arctic marine primary productivity (19), affecting zooplankton production and that of the arctic cod that feed on them (20) as well as their seabird and marine mammalian predators (2, 21) (Fig. 1B).

Warming-related reductions in sea-ice thickness and snow cover on sea ice in the Arctic Ocean have also been associated with increased sub-ice primary production. A midsummer phytoplankton bloom below the sea ice in 2011 was attributed to enhanced light transmission through a thin layer of first-year ice (22). Hence, replacement of thick, multiyear ice by thin, first-year ice as the Arctic warms may contribute to increases in the frequency and magnitude of algae and phytoplankton blooms. However, the roles of sea-ice loss and ocean freshening in the tradeoffs between light versus nutrient limitation of arctic marine primary productivity remain poorly understood (1). Freshening of the euphotic layer associated with sea-ice melt may ultimately reduce nutrient availability for phytoplankton, limiting their productivity despite increased solar input with sea-ice retreat (23). Also, increased solar irradiance of sea-ice algae through thinning ice reduces their fatty acid content and quality as forage for marine copepod grazers (24). Furthermore, freshening of the Arctic Ocean due to increased meltwater from sea ice and runoff from coastal rivers is associated with the replacement of larger nanoplankton by smaller picoplankton, reducing the efficiency of seasonal energy transfer in marine food webs (25).

Vertebrate species dependent upon sea ice for foraging, reproduction, and resting are also directly affected by sea-ice loss and thinning (3). Examples

of marine vertebrates adversely affected by sea-ice decline and longer ice-free seasons include declines in body condition and abundance of polar bears (26) and loss of critical habitat for reproduction and offspring provisioning by ringed seals (27). Pacific walrus have recently displayed greater use of shoreline haul-out areas and declining abundance in portions of their range, as retreating near-coastal sea ice has reduced their access to critical shallow water foraging from the ice edge (28). Mass

mortality among Pacific walrus along the coast of the Chukchi Sea in Alaska has been attributed to loss of sea ice over the continental shelf (29).

Indirect Effects of Sea-Ice Loss

Sea-ice loss may also influence ecological dynamics indirectly through effects on movement, population mixing, and pathogen transmission. For populations and species currently isolated only during the summer ice-free season in the

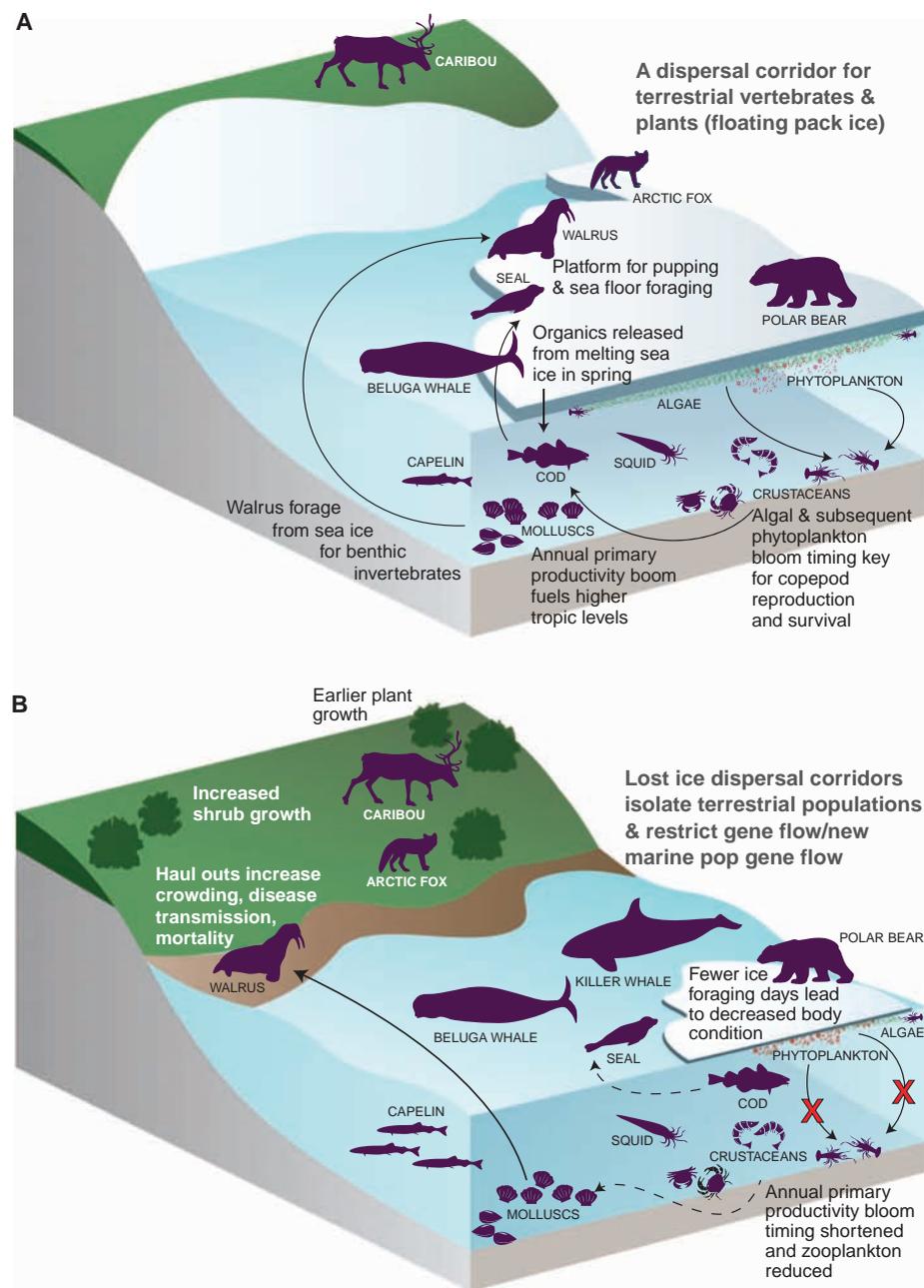


Fig. 1. Ecological interactions influenced by sea ice. The sea-ice biome influences the abundance, distribution, seasonality, and interactions of marine and terrestrial species by its presence (A). It is unique for its complete seasonal disappearance in portions of its distribution. Lengthening of this annual period of absence and an overall decline in ice extent, thickness, and stability will have considerable consequences for these species and interactions (B).

Arctic, declining annual presence of sea ice will reduce trans-ice and interisland migrations outside of the summer season. Sea-ice loss and a lengthening of the ice-free season will thus increase genetic isolation among populations of such species. Sea ice is the strongest predictor of genetic differentiation among arctic fox populations (30). In the Canadian Arctic Archipelago, interisland and island-mainland migration can promote genetic rescue of isolated wolf populations (31). The loss of sea ice that seasonally connects these populations will render such genetic rescue increasingly unlikely.

In species for which sea ice acts as a barrier to dispersal, its loss and a lengthening of the ice-free season will increase population mixing, reducing genetic differentiation. Perennial sea ice likely maintains genetic divergence between North Pacific and North Atlantic populations of walrus (32) and some whales (33). Loss of sea ice will also increase contact among closely related species for which it currently acts as a barrier to mixing, in-

creasing the likelihood of hybridization. For instance, at least seven pairs of arctic and subarctic marine mammals hybridize, and many more hybridizations are expected with sea-ice loss (34). Observed hybridization between polar bears and grizzly bears may be the result of increasing inland presence of polar bears as a result of prolonged ice-free seasons (34). Loss of sea ice may reduce arctic faunal diversity if it promotes hybridization among populations, species, and genera currently isolated by ice (34).

Arctic warming and sea-ice loss will also facilitate invasions by new hosts, pathogens, and disease vectors. The projected decrease in sea-ice cover in arctic Canada will increase contact between eastern and western arctic species, promoting mixing of pathogen communities previously isolated. Phocine distemper virus, currently endemic to pinnipeds of the eastern Arctic, may spill over to western arctic species where it is currently absent. Mixing of Atlantic and Pacific pathogen communities that have been ecolog-

ically and evolutionarily isolated may be expected across a range of marine species, with important implications for the health of populations previously not exposed to them. For walrus, reduced sea-ice cover forces increased use of shoreline haul-outs (Fig. 1B), increasing the local density of animals. This promotes transmission of environmentally and density-dependent pathogens. Additionally, increased time spent on land by marine species may enhance transmission of pathogens between them and terrestrial species (35).

Changes in animal behavior as a result of sea-ice loss may also alter patterns of pathogen exposure. In the Canadian Arctic, later freeze-ups and increased shipping traffic could shift or prevent the annual migration of the Dolphin and Union caribou herd. Because migration poses benefits for reducing parasitism, such a change may increase parasite loads in this herd. Conversely, sea-ice loss may be beneficial in preventing pathogen introduction and disease epidemics to island ecosystems in cases where sea ice provides a corridor for pathogen transmission. Sporadic outbreaks of rabies on Svalbard are attributed to introduction by arctic foxes traversing sea ice from the Russian mainland (36). Reduction in sea ice would likely minimize or eliminate this movement.

Shifts in feeding ecology mediated by sea-ice loss may also alter the community of parasites within a host, particularly in the case of parasites with complex life cycles (37). For example, the diet of thick-billed murres in Hudson Bay has shifted from arctic cod to capelin (38), potentially affecting the occurrence of parasites transmitted through the food web. Similarly, sea-ice alteration of exposure of wildlife to environmental toxicants will have important impacts on the immune function of animal species and their ability to cope with existing and new pathogens (35).

Effects on Terrestrial Systems

Contributions of sea-ice loss to near-surface warming over land across the Arctic (13) indicate that earlier annual sea-ice melt and ice loss will influence seasonality in terrestrial systems. Local warming over land adjacent to areas of sea-ice loss is expected to increase terrestrial primary production for two reasons: Surface warming advances arctic soil thaw dates and delays soil freeze dates (39), and sea-ice loss is expected to promote permafrost warming up to 1500 km inland from the coastline (40).

In West Greenland, long-term monitoring of plant phenology at an inland site indicates a close association between the annual timing of the plant growing season and sea-ice extent (Fig. 3A) (41). Here, springs with low sea-ice extent are characterized by early green-up of vegetation. Advancement of the timing of the spring pulse of primary production, in turn, exacerbates trophic mismatch for caribou at the site (41), as it does for copepod grazers in the marine food web (17). At the same inland site, abundance of dwarf shrubs has

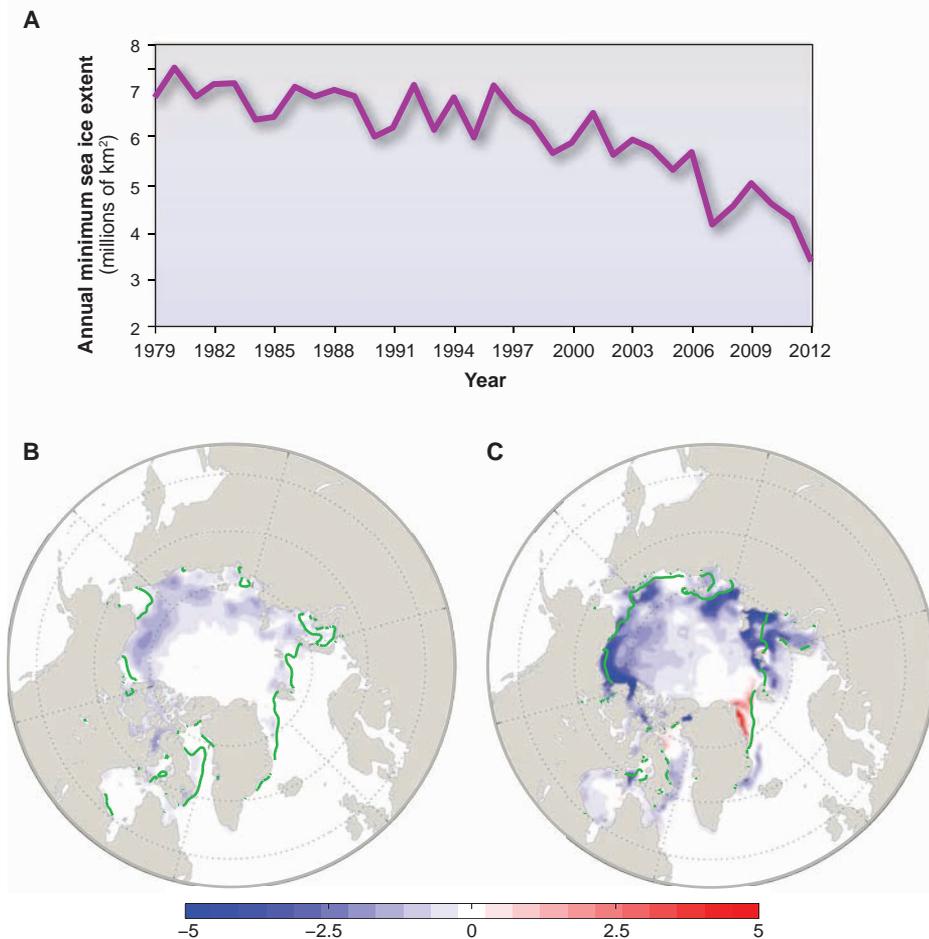


Fig. 2. Trends in arctic sea ice through time and space. Annual minimum sea-ice extent (A) has declined dramatically from 1979 to 2012. The percentage concentration loss per year in seasonal sea-ice minimum extent (July to September) has increased most between 1979 and 1999 (B) and between 2000 and 2011 (C) along the coasts of Russia, Alaska, and the Canadian Archipelago. The color bar indicates the direction of the sea-ice trend in percentage change per year; in the panels, the mean 15% concentration contour is shown in green. All data is from NASA Distributed Active Archive Center at the National Snow and Ice Data Center.

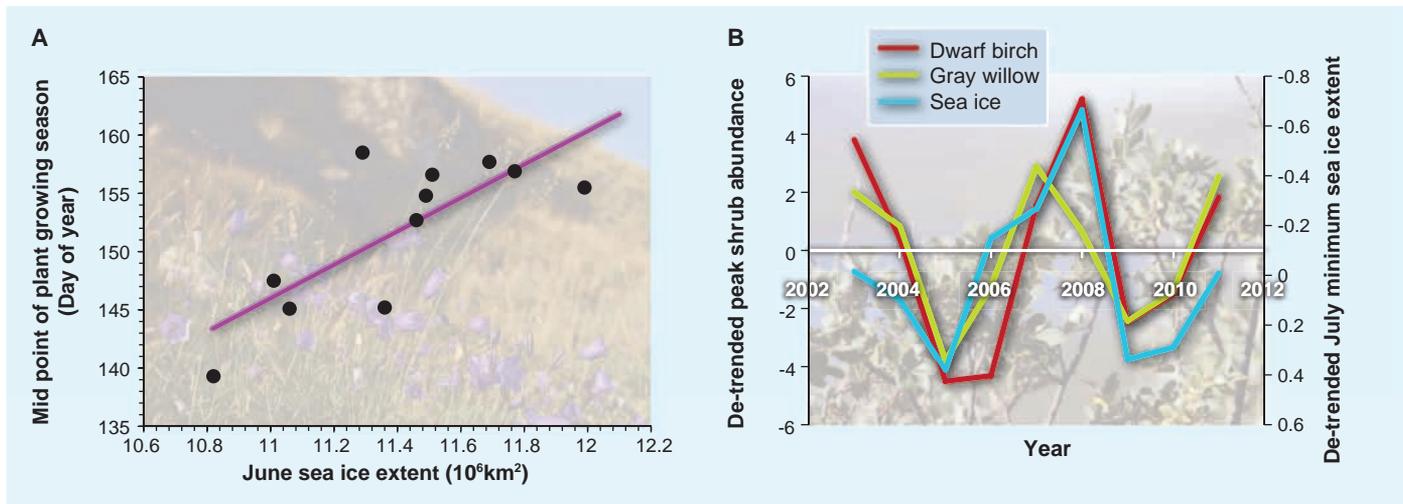


Fig. 3. Relations between sea ice and timing and abundance of terrestrial plant growth. (A) The annual midpoint of the plant growing season at an inland site in Greenland, when 50% of species have emerged on plots monitored between 1993 and 2011, is closely associated with Arctic-

wide sea-ice extent in June [data from (41)]. **(B)** Detrended annual peak aboveground abundance of dwarf shrubs [data from (42)], which have been increasing at the same site (42), displays a close association with July sea-ice extent in the previous year.

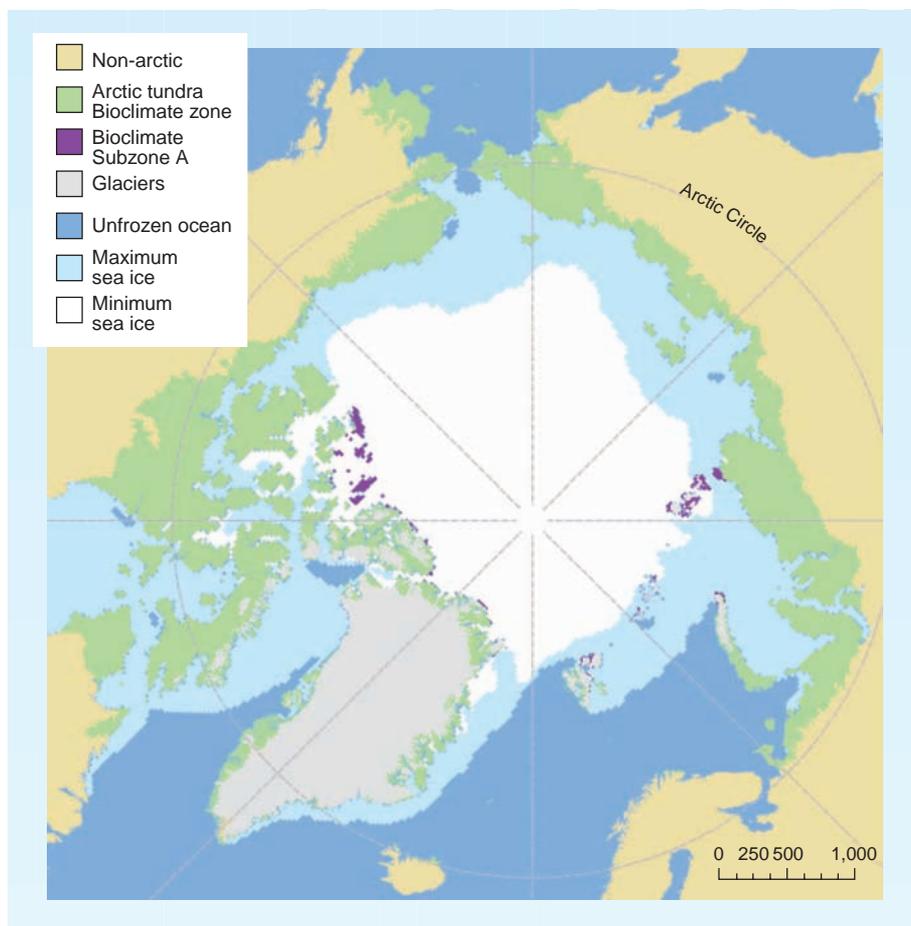


Fig. 4. Arctic terrestrial vegetation zones in relation to sea ice. The extent and locations of the arctic tundra bioclimate zone and bioclimate subzone A [boundaries of both from (44)] are closely related to the climatological maximum and minimum spatial extent of sea ice. The mean (1982 to 2010) maximum ice boundary (50% ice cover) is shown for week 22 (1 June), and the minimum ice

boundary (50% ice cover) is shown for week 35 (1 September). The tundra extent generally corresponds to the extensive presence of sea ice during the late winter and spring. Bioclimate subzone A relates to the presence of extensive ice cover during all of the summer and early autumn (45). Ice boundaries were determined from passive microwave data averaged for 1982 to 2012.

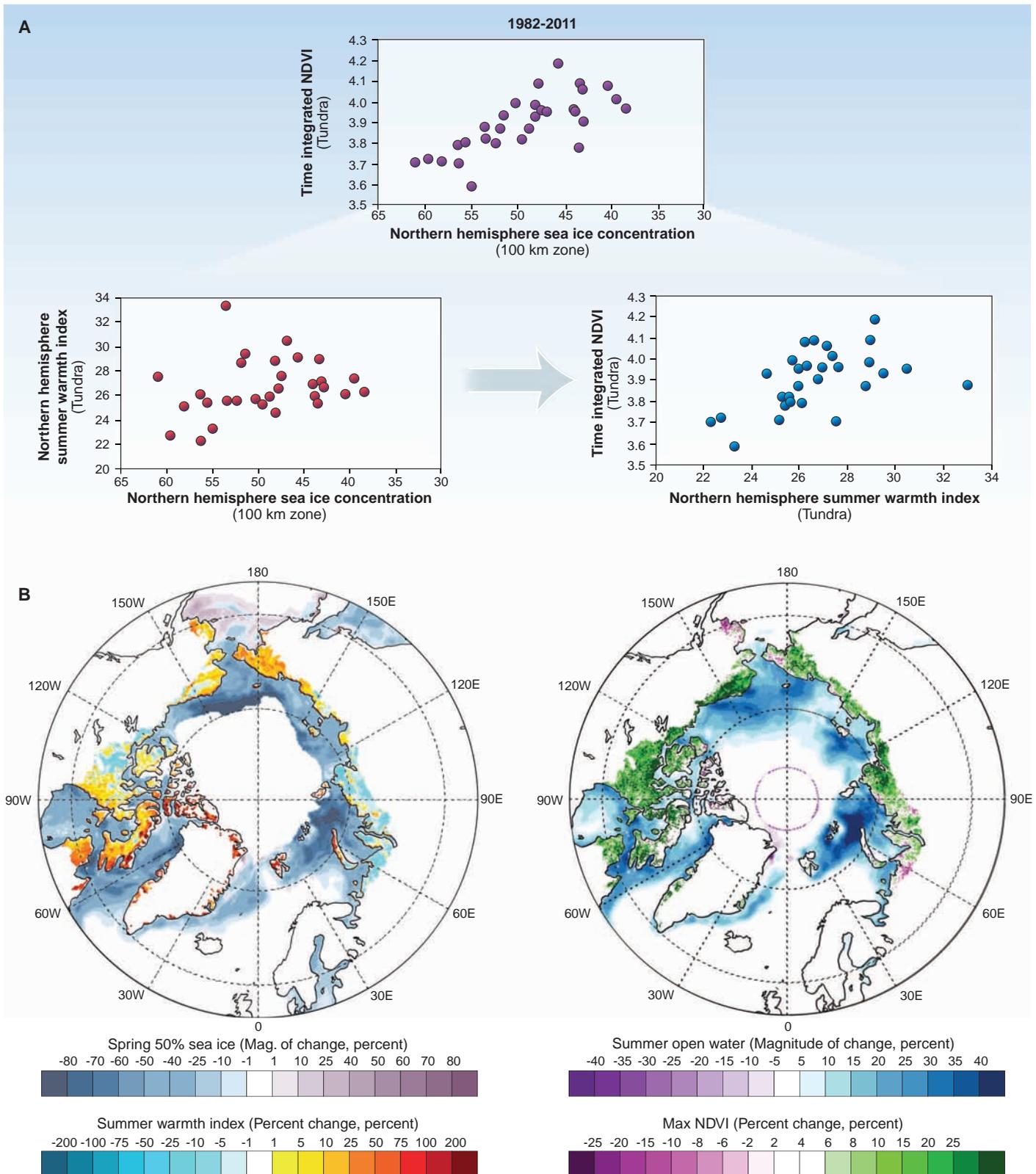


Fig. 5. Increasing arctic terrestrial primary production associated with sea-ice decline. (A) Coastal tundra primary productivity, shown as time-integrated NDVI, has increased in association with declining arctic sea-ice concentration or area (top). This is presumed to be driven by the relations between

sea-ice area and SWI (bottom left) and between SWI and NDVI (bottom right). (B) Pan-Arctic trends in SWI (left) and NDVI (right) [adapted from (4, 5)] vary spatially across the Arctic, but almost all locations experienced an increase in maximum NDVI and an increase in summer open water (right).



increased (42) and relates inversely to sea-ice extent during the previous growing season (Fig. 3B). Inferring causality between correlated time series is difficult but may be supported when the response displays a lagged relation to the presumed driver, as in this instance.

Increases in the abundance and cover of shrubs are occurring across the Arctic (43). In coastal and near-coastal areas, these increases are likely related to local warming driven by sea-ice loss. The entire arctic tundra biome is coupled with the marine system because of its extensive coastline (Fig. 4) and is especially vulnerable to sea-ice decline because of the strong climatic influence of the nearby sea ice. A unique area that will be particularly sensitive to sea-ice loss is bioclimate subzone A (Fig. 4) (44). Floristically depauperate and experiencing some of the largest and fastest temperature changes in the Arctic, this zone is likely to experience complete loss of summer sea ice in the next few decades, rendering it an endangered bioclimate subzone (45).

Associations between sea-ice decline and terrestrial primary productivity are also evident at larger scales across the Arctic. Biome-scale evidence for a relationship between sea-ice decline and increases in terrestrial primary productivity derives mainly from satellite data. Between 1982 and 2011, as near-coastal sea-ice area declined, the summer warmth index (SWI) for low-elevation tundra along the Arctic Ocean increased, precipitating an increase in vegetation production captured by Normalized Vegetation Difference Index (NDVI) data (4, 5) (Fig. 5A). The relationship between SWI and sea-ice extent is largely negative for the entire Northern Hemisphere, indicating warming associated with sea-ice loss, but varies among regions such as Eurasia and North America (fig. S1). Moreover, NDVI trends and relations to sea-ice extent vary across the Arctic (46) (Fig. 5B), suggesting that other factors likely interact with abiotic drivers associated with sea-ice loss to influence variation in terrestrial primary productivity across the tundra biome.

Increases in terrestrial primary productivity related to sea-ice decline and the consequent increase in land surface temperatures have the potential to alter ecosystem carbon flux (47). Modeling of measurements of CO₂ flux from West Greenland indicates a doubling of carbon uptake concordant with shrub increases there between 2003 and 2010 (48). Moreover, ecosystem process models indicate increases in arctic tundra methane emissions matching sea-ice fluctuations and trend for the period from 1979 to 2006 (47). Projecting carbon dynamics in terrestrial systems with future sea-ice declines is, however, complicated by the unknown extent to which respiration may increase with warming (47). A recent link between sea-ice decline and the annual extent of tundra fires in Alaska (49) also suggests that ice loss may contribute to periodic massive pulses of terrestrial carbon release.

Future Challenges

Despite numerous examples of effects of declining sea ice on dynamics, abundance, and interactions among species, foreseeing the consequences of continued sea-ice loss remains difficult. A considerable challenge is to assign attribution, with greater certainty, to sea ice as a driver of ecological dynamics. The associations that we have drawn are weakened by reliance on patterns of covariation between sea-ice dynamics and ecological dynamics. Increasing emphasis on sea-ice decline as a contributing factor to regional warming (11) will improve the potential for increased recognition of sea-ice decline as a driver of ecological dynamics (4, 45). The field of joint attribution (50) in studies of ecological response to climate change can be informative here. Joint attribution is a statistical approach for assigning causation by anthropogenic forcing in recent warming and causation by warming in observed ecological dynamics (50). Further development and application of this approach will improve our ability to detect ecological responses to sea-ice decline.

A second challenge is to foresee and anticipate the human dimension as sea-ice decline increasingly facilitates access to coastal and near-shore areas for increased industrial development and extended-season shipping. In the Arctic, loss and thinning of sea ice is anticipated to increase accessibility of near-coastal and remote marine zones of all eight arctic nations by up to 28% by the middle of this century (51). Increased human access to formerly remote areas of the Arctic could have negative consequences for many species and their habitats, including those exploited by humans. Increased marine access will also likely accelerate the pace of arctic mineral and petroleum exploration in both terrestrial and marine systems (52), with increased threats to marine species such as bowhead whales (53) and Pacific walrus (51). Viewing sea ice as an important indicator of climatic warming and as an integrator and driver of ecological dynamics in the Arctic will improve our understanding of the systems-level functioning of this region and our basis for anticipating and responding to further change.

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Supplementary Materials
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Fig. S1
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