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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.

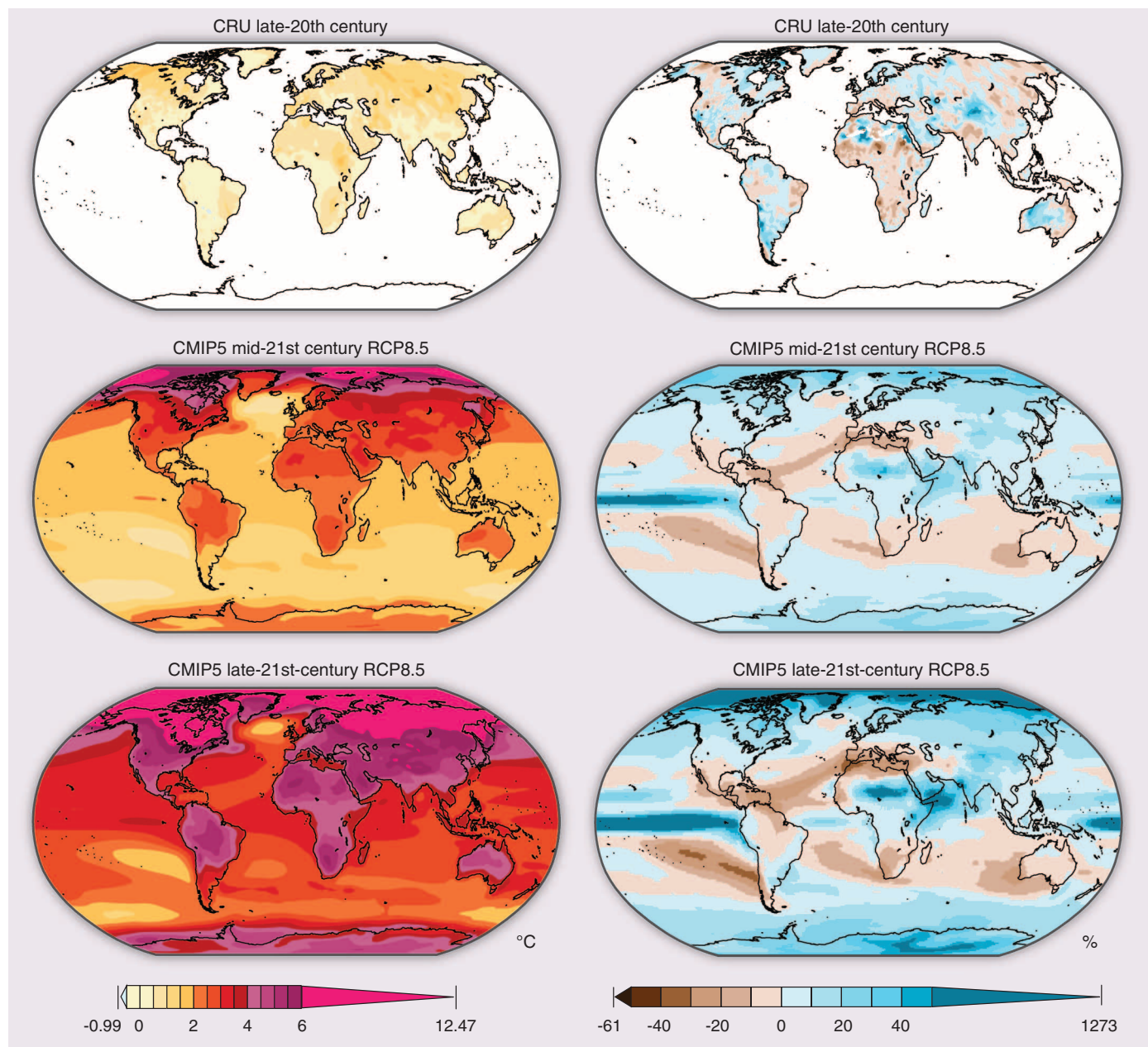


Fig. 1. Observed and projected changes in annual temperature and precipitation. (Top) Climatic Research Unit (CRU) observations (which are available only over land), calculated as 1986–2005 minus 1956–1975. (Middle) Differences in the mid-21st-century period of the CMIP5 RCP8.5 ensemble, calculated as 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), whereas the occurrence of daily-scale cold extremes

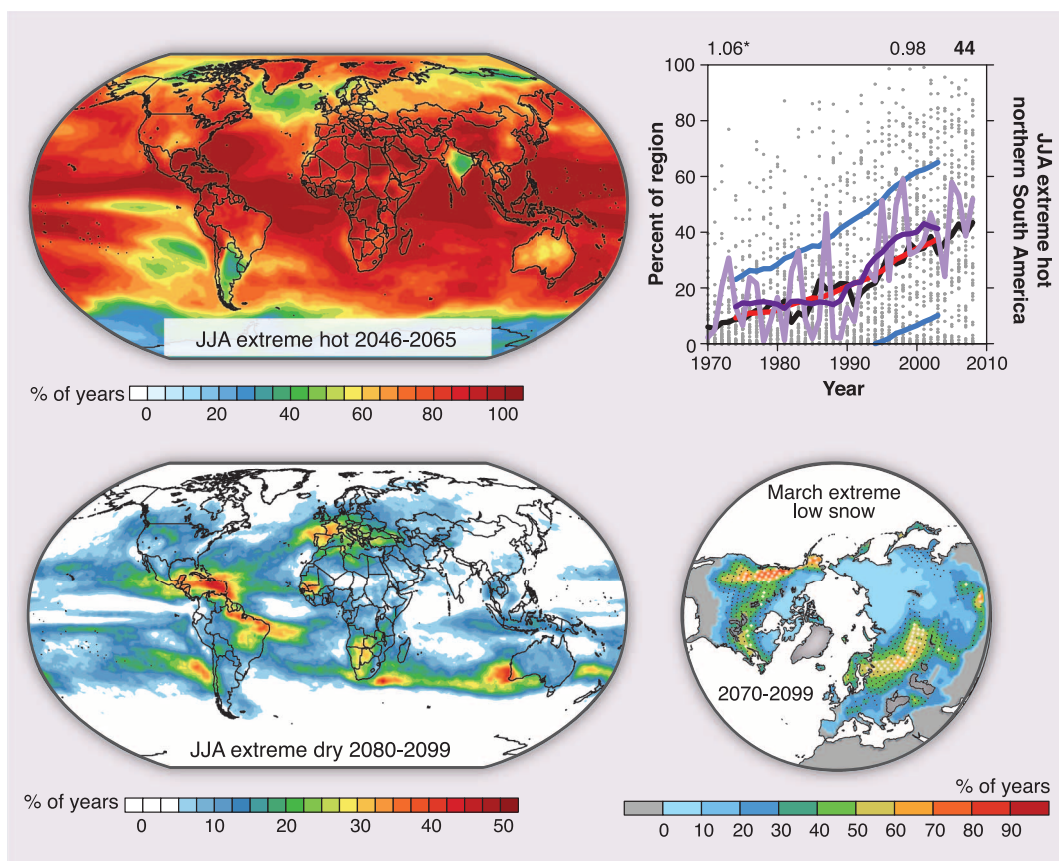


Fig. 2. Changes in seasonal extremes. (Left) The frequency of the 1986–2005 maximum June–July–August (JJA) temperature (top left) and minimum JJA precipitation (bottom left) in the 2046–2065 and 2080–2099 periods of RCP8.5 [from (65)]. (Bottom right) The frequency of the 1976–2005 minimum March snow 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

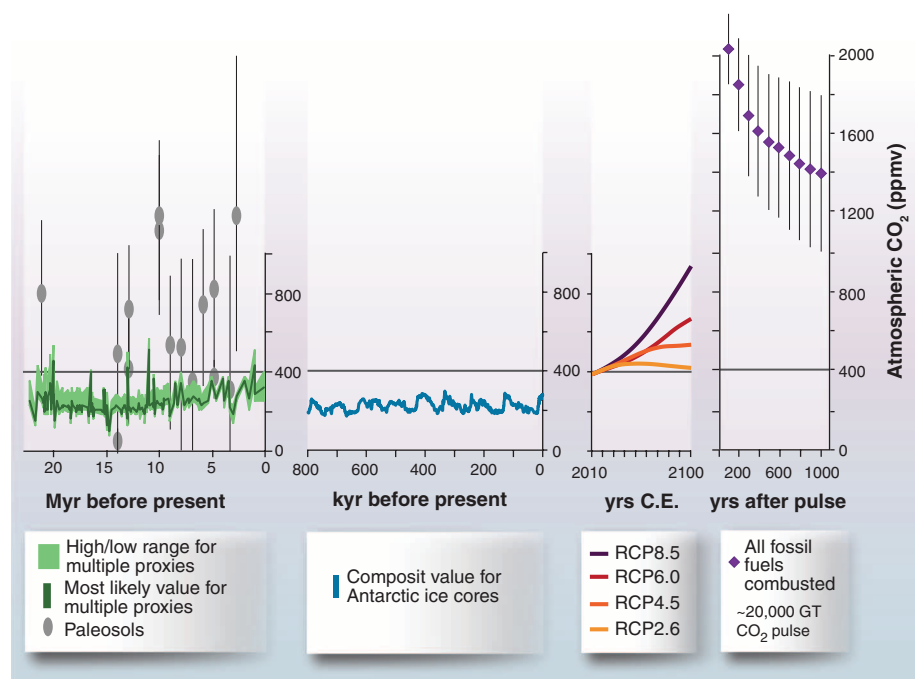


Fig. 3. Past and potential future atmospheric CO₂ concentrations. (Left) The high-low range of CO₂ over the past 22 million years from phytoplankton/forams, stomatal indices/ratios, and marine boron (105). (Middle left) CO₂ from Antarctic ice cores (103). (Middle right) CO₂ concentrations for different 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.

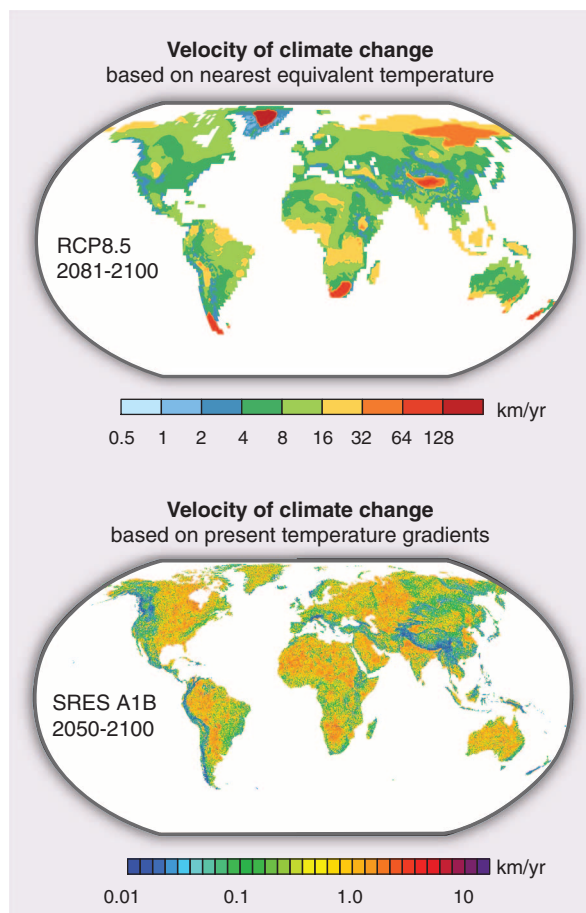


Fig. 4. The velocity of climate change. (Top) The climate change velocity in the CMIP5 RCP8.5 ensemble, calculated by identifying the closest location (to each grid point) with a future annual temperature that is similar to the baseline annual temperature. (Bottom) The climate change velocity [from (117)], 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 Materials

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Materials and Methods

Fig. S1

Table S1

References (132–135)

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REVIEW

Marine Ecosystem Responses to Cenozoic Global Change

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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 (pCO₂) 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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