Paleoclimate perspectives on contemporary climate change

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Paleoclimate Perspectives on Contemporary Climate Change

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Keywords

paleoclimate, abrupt climate changes, terrestrial ecosystem responses, biodiversity, biospheric feedbacks, data–model integration

Abstract

Paleoclimate data have informed contemporary climate science, and could do so more extensively. Quaternary data record glacial–interglacial cycles paced by variations in Earth's orbit. Faster climate changes include repeated warming–cooling (Dansgaard–Oeschger) cycles during glacial times as well as abrupt glacial terminations, suggesting repeated crossings of a tipping point. Climate models reproduce some key features of past climate change but not others, including patterns of orbitally forced precipitation changes and linkages between different modes of climate variability. Land ecosystem records document plant species' resilience to rapid climate change, in contrast to large mammals' vulnerability; multiple

roles of natural wildfires; and effects of low glacial CO_2 on vegetation and fire. Dansgaard–Oeschger cycles constrain biogeochemical feedbacks, showing large increases of CH_4 and N_2O with warming and suggesting destabilizing feedbacks through land surface albedo under glacial conditions. Lessons for conservation include recognizing "novel" ecosystems as normal and respecting the paramount role of species movements as responses to rapid climate change.

Contents

1. INTRODUCTION

Quaternary: the past 2.58 Myr, characterized by alternations of glacial and interglacial periods paced by changes in Earth's orbit

Glacial–interglacial cycles: alternations of glacials (large continental ice sheets, low CO_2, cold climate) and interglacials (reduced ice sheets, high CO_2, warmer climate)

Climate science has become a high-profile, transdisciplinary field, spurred on by pressure to understand and predict contemporary climate change and its consequences. It draws on mathematics, physics, chemistry, biology, social sciences, and economics and relies on both large observational data sets and advanced computational models. Most climate science focuses on timescales of years to centuries, using instrumental weather records and space-borne measurements to test and improve models that are then used for scenario predictions of future climate.

Paleoclimate science emerged from a different background, analyzing the nature, controls, and impacts of climate change on timescales from centuries to millions of years (1). A large subfield is dedicated to the Quaternary period [the past 2.58 million years (Myr), characterized by glacial–interglacial cycles and the emergence of modern humans] and especially the Holocene [the past 11.7 thousand years (kyr), after the abrupt termination of the last glacial period]. Paleoclimate science is transdisciplinary, drawing on multiple data sources and, increasingly, climate models. Paleoclimate science has provided key insights into contemporary climate change through its ability to provide tests for models under conditions substantially different from those to which they have been tuned (referred to as out-of-sample tests; 2), observations that illuminate climate phenomena (such as global tipping points and extremely cold or warm states) far outside anything experienced during the period covered by direct measurements (1, 2), information about impacts on biodiversity, and unique information about the environmental context of human prehistory.

Holocene: past 11.7 kyr; the interglacial following the rapid termination of the last ice age, characterized by the invention of agriculture

Cenozoic: the current geological era (the past 66 million years), with plants and animals broadly similar to those of today

Interactions between the paleoclimate and mainstream climate science communities have been limited. Coverage of paleoclimate topics in Intergovernmental Panel on Climate Change (IPCC) reports has been notably patchy. In the First Assessment Report (3), mid-Holocene climate was incorrectly presented as an analogy for future "greenhouse" climate. The Fifth Assessment Report (4) dealt with some key paleoclimatic phenomena in a dedicated chapter (5), but almost none of its insights were included in the Technical Summary (6). The Sixth Assessment Report (7) attempted to "mainstream" paleoclimate but showed only global or hemispheric mean temperatures—arguably underrepresenting the regional complexity of natural climate change (8).

In this review, we first summarize the main sources of data on past climates, then focus on ways in which data from the past have contributed to our current understanding of climate processes, ecosystem responses, and biosphere feedbacks. We discuss some of the key properties and limitations of paleodata as well as the roles of paleoclimate modeling in the broader context of climate science. We conclude by suggesting ways in which the understanding and prediction of climate could be furthered by stronger exchanges between the two communities. We focus primarily on land climates, although we refer to marine and ice-core records of climate change wherever needed. We restrict our attention to the Cenozoic (the past 66 Ma, the period since the last great extinction event that eliminated the dinosaurs), with an emphasis on the Quaternary.

2. SOURCES OF PALEOCLIMATE DATA

Climate influences atmospheric composition, the hydrological cycle, and marine and terrestrial biology. Records of climate changes are preserved in natural archives and, provided that they can be dated with sufficient accuracy, can be used as "sensors" of climatic and environmental change (1). Sources of paleoclimate data include polar and montane ice cores, deep-sea sediments, lake sediments, peat, loess deposits, speleothems, tree-ring series, and animal middens (9) (see the **Supplemental Material** for a fuller description of different sources; see also **Supplemental Table 1**). These various archives have different characteristic spatial scales. Ice-core records provide global signals and some local records of global relevance such as polar temperatures (10). Marine records provide mainly local or regional signals but describe an interconnected system that encourages a global perspective (e.g., 11). Terrestrial records provide local or regional signals; records from multiple sites need to be combined in order to extract meaningful inferences about climate (e.g., 12, 13) The timescales of different kinds of records also vary. Tree-ring records can provide information on annual or subannual timescales (14), but individual series span only decades to centuries; millennial-scale records are obtained by stitching together overlapping series. Speleothems and annually laminated lake sediments can also provide annual or subannual resolution (15, 16), but most cover only a few millennia. Lake sediments, peat, and loess can provide much longer records, in some cases continuous records over 0.5 Ma or longer (**Supplemental Table 2**), but with lower temporal resolution (decades to centuries). There is good coverage of terrestrial records for the Holocene over most of the world, but data coverage becomes sparse further back in time. Fewer than 100 pollen records cover some part of the last glacial period with sufficient resolution to detect millennial-scale climate variability (17).

Supplemental Material >

Terrestrial paleorecords can provide geochemical or isotopic data on aspects of environmental change (see the sidebar The Most Important Isotope Measurements in Quaternary Research).

THE MOST IMPORTANT ISOTOPE MEASUREMENTS IN QUATERNARY RESEARCH

The radioactive isotope ^{14}C is produced continuously by cosmic-ray bombardment of ^{14}N, and incorporated into plants during photosynthesis. Due to its decay (with a half-life > 5,000 years) ^{14}C is useful for dating organic materials up to about 50,000 years old. In addition, many stable isotopes are used as paleoenvironmental indicators. Most important are the heavy isotopes of oxygen (^{18}O) and carbon (^{13}C). Evaporation depletes ^{18}O in water vapor (and therefore in precipitation) and enhances ^{18}O in the remaining water. Therefore, ^{18}O in the $CaCO_3$ shells of benthic foraminifera in deep-sea cores yields a record of global ice volume. The fractionation is temperature-dependent, so ^{18}O in ice cores (and speleothems) also record past temperatures. Photosynthesis discriminates against ^{13}C; the strength of discrimination depends on the photosynthetic pathway (weaker in C_4 than C_3 plants) and the ratio of leaf-internal to ambient CO_2, a key variable determining the rate of photosynthesis. ^{13}C measured in benthic foraminifera yields a record of changes in global land carbon storage; ^{13}C in materials of land-plant origin records their photosynthetic pathway and the extent to which photosynthesis is limited by stomatal closure, e.g., in response to atmospheric dryness.

Supplemental Material >

Phylogenetic niche conservation (PNC): the tendency of lineages to retain traits related to their environmental tolerances through speciation events and over macroevolutionary time

However, the most detailed information comes from biotic assemblages. Past climates are inferred from a wide variety of biotic assemblages, including marine (e.g., foraminifera, diatoms, mollusks), freshwater and wetland (e.g., diatoms, chrysophytes, chironomids, testate amoebae), and terrestrial organisms (e.g., plants, insects, mammals). Paleoclimate reconstructions are facilitated by statistical methods (18) (**Supplemental Table 3**), which capitalize on the principle of phylogenetic niche conservatism (PNC) (19, 20) (see sidebar Niche Conservatism and **Supplemental Figure 1**). PNC is evidenced by taxa occupying similar climates in disjunct distributions across different continents (21) and the fact that modern distributions of widespread tree genera can be predicted using climate–pollen relationships developed from other regions (22).

3. CLIMATE PROCESSES

3.1. Drivers of Natural Climate Change

The drivers of climate change on different timescales are well-established, even if not all the mechanisms are completely understood. The Cenozoic was characterized by declining CO_2, thought to be caused by an imbalance between the long-term sink (chemical weathering) and source (volcanism) of CO_2, accompanied by global cooling (**Figure 1**). The decline in CO_2 and global mean

NICHE CONSERVATISM

Niche conservatism is a concept in evolutionary biology, whereby the environmental tolerances of most species, constrained by genetics, phylogeny, developmental pathways, and evolutionary tradeoffs, evolve more slowly than rates of environmental change. Thus, under niche conservatism, species track climatic changes by shifting their ranges to more suitable habitats rather than evolving to adapt to the new conditions (**Supplemental Figure 2**). Environmental tolerances and responses are part of larger, organism-level suites of integrated morphological, anatomical, physiological, and behavioral traits that are difficult to change in toto without costs to fitness in the form of inefficiencies and vulnerabilities. Most species have some capacity for adaptive evolution to climatic change, but it is generally limited in scope, particularly to climate changes of the rates and magnitudes experienced in the Quaternary. Niche conservatism can be deeply rooted in phylogeny, with sister clades on different continents occupying similar climates.

temperature began around 55 Ma and proceeded (with interruptions) into the Quaternary period, which has been characterized by alternation of glacial and interglacial conditions. Superimposed on the long-term trends are the so-called Milankovitch cycles, caused by variations in Earth's orbit with approximate periodicities of 100 kyr (eccentricity), 41 kyr (obliquity), and 19–23 kyr (precession, i.e., changes in the season when the Earth is closest to the Sun). These frequencies are ubiquitous in long Quaternary time series. Glacial–interglacial cycles were dominated by the

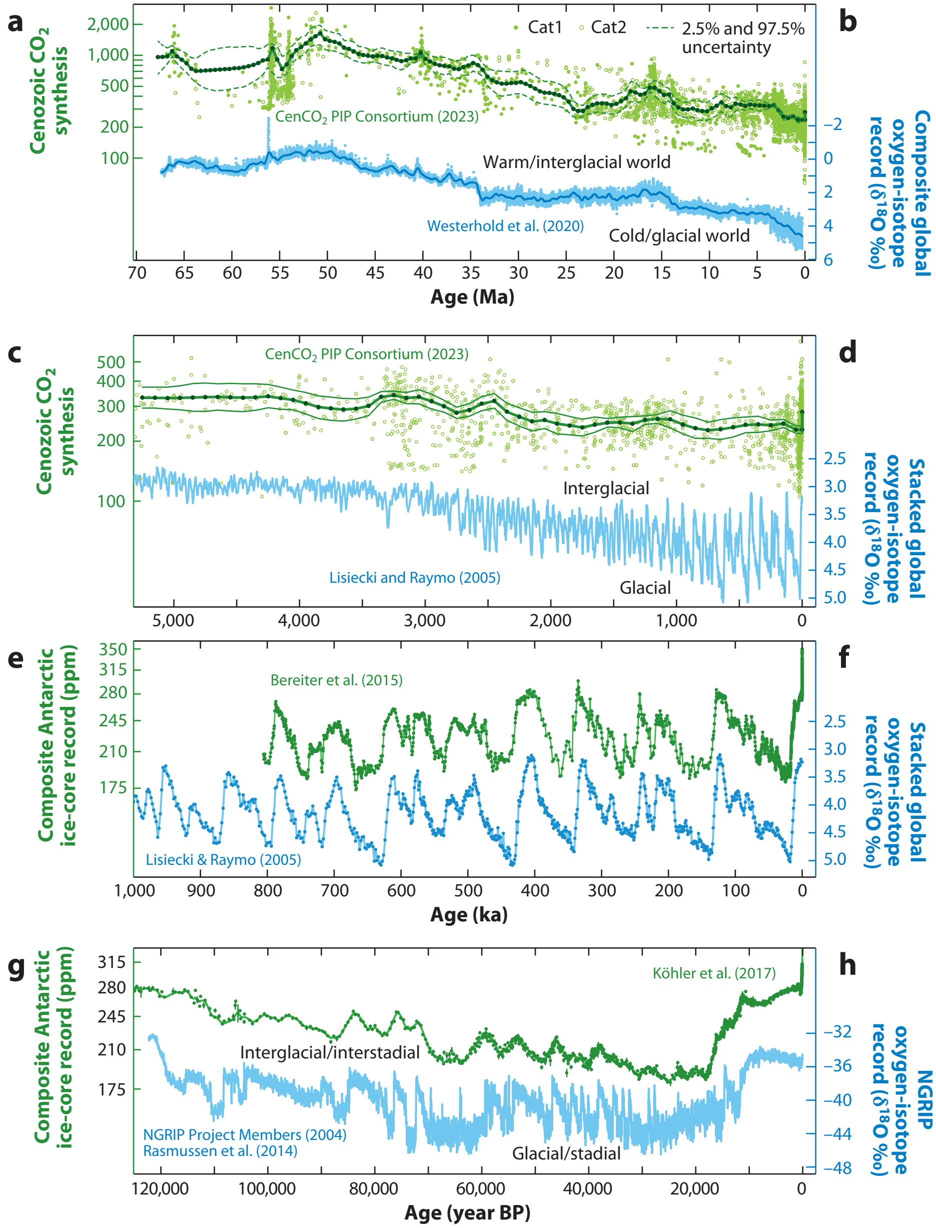

Figure 1

(*Continued*)

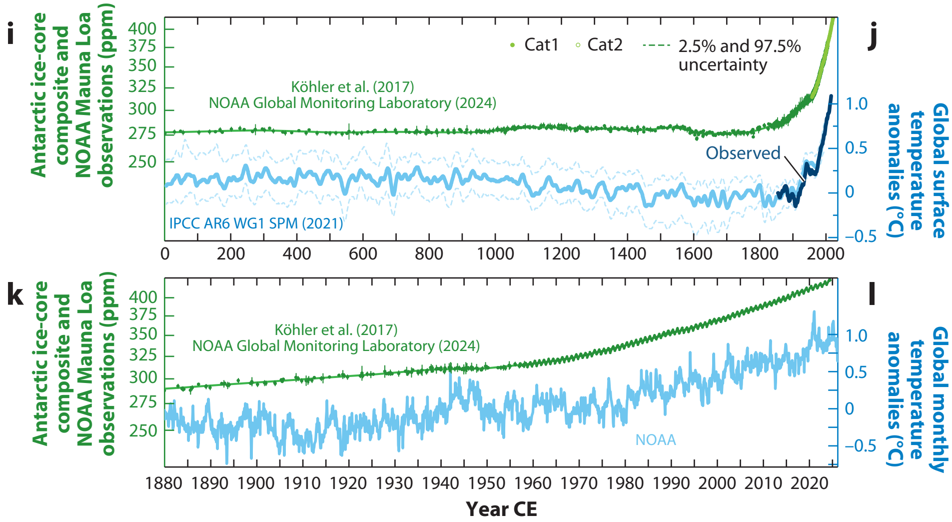

Figure 1

Variability of CO_2 and temperature on multiple timescales. CO_2 is plotted on a $\log_{10}$ scale to reflect the scaling of its radiative forcing effect with respect to its concentration. (*a*) Cenozoic (last 70 million years, Myr) CO_2 synthesis (146), Cat1 (*solid dots*), and Cat2 (*open circles*) point data, where Cat1 represents estimates based on data with fully quantified uncertainties and Cat 2 represents data with sources of uncertainty that are not fully constrained; and 500 kiloyear (kyr) smoothed data (*connected dark green dots*) with 2.5% and 97.5% uncertainty values (*thin lines*). (*b*) Temperature record for the past 70 Myr based on a global compilation of oxygen-isotope (^{18}O) records, a general indicator of global temperatures (147). The solid blue line represents a loess smoothed curve fit to individual data points. (*c*) As in panel *a*, but only for the past 5 Myr. (*d*) Stacked global oxygen-isotope ($\delta^{18}O$) record (148). (e) Composite Antarctic ice-core record over the past 800 kyr (149). The data include twentieth-century observed atmospheric concentrations. (*f*) As in panel *d*, but only for the past 1,000 kyr. (*g*) Composite Antarctic ice-core record over the past 125 kyr [year b2k = years before 2000 common era (CE)] (122). This record also includes twentieth-century values. (*h*) The $\delta^{18}O$ record from the North Greenland Ice Core Project (NGRIP) ice core (150, 151) plotted as 50 year mean values over the past 125 kyr. (*i*) Antarctic ice-core composite (122) merged with National Oceanic and Atmospheric Administration (NOAA) Mauna Loa observations (152) for the past 2,000 years. (*j*) The decadally resolved temperature-anomaly reconstructions [deviations from a 1950–1900 CE base period)] for the past 2,000 years from the Intergovernmental Panel on Climate Changes Sixth Assessment Report (IPCC AR6) Working Group 1 Summary for Policymakers (SPM) (153). The dark blue line is a smoothed version of observations from 1850–2020 CE. (*k*) As in panel *i*, for 1850–2024 CE. The NOAA Mauna Loa data begin in 1958 CE and are shown as monthly values superimposed on the deseasonalized trend. (*l*) NOAA global monthly temperature anomalies (deviations from a 1900–2000 CE base period). (154). The curves illustrate that climate is always varying and has no average value but often varies within a particular window. The curves also show the rich set of trends, periodic and quasi-periodic variations, and abrupt changes that both require explanation and provide natural experiments to test models.

Milankovitch cycles/ orbital forcing: quasi-periodic changes in Earth's orbit causing changes in the latitudinal and seasonal distribution of incoming solar radiation

41 ka frequency until around 0.7 Ma [the mid-Pleistocene transition (MPT)], when the 100 ka frequency became increasingly dominant. The response of the climate system to orbital forcing since the MPT has been highly nonlinear and characterized by abrupt transitions (terminations) at the end of each glacial interval.

Different mechanisms are responsible for faster variations in climate, superimposed on the Milankovitch cycles. These include the millennial-scale Dansgaard–Oeschger (D-O) cycles during glacial times as well as more rapid variations linked to solar output, volcanic eruptions, and modulations of the internal variability modes such as the El Niño–Southern Oscillation (ENSO). These phenomena are discussed further below.

3.2. Climate Sensitivity

Paleoclimate evidence provides information about climate processes that are important for understanding potential future climate changes. Current assessments of the steady-state global temperature increase for a doubling of CO_2 (the equilibrium climate sensitivity), for example, rely in part on paleoclimate evidence about the climates of the Paleocene–Eocene Thermal Maximum (PETM), mid-Pliocene, and Last Glacial Maximum (LGM) (23). Estimates based on paleoclimate converge with other lines of evidence, leading to a substantial reduction in uncertainty regarding this key quantity and effectively ruling out the possibility that the equilibrium climate sensitivity is less than 1.5 K or more than 4.5 K (23, 24).

3.3. Abrupt Climate Changes and Tipping Points

The paleoclimate record provides evidence of abrupt climate changes that have no recent parallels. The PETM is often cited as an example, but its abruptness remains disputed (25). Glacial terminations, however, are indeed abrupt. While the global transition from full glacial to full interglacial state may take up to 10 kyr due to the slow pace of ice-sheet melting, most of this change (in terms of climates on ice-free land) is accomplished over a few decades (26)—as was the case with abrupt warming at the end of the Younger Dryas in the last termination. Glacial terminations are archetypical examples of global tipping points being crossed. But although there has been speculation (27) about a possible future global tipping point (into a "hothouse world") the paleorecord does not provide any analogs for such a phenomenon, and the conditions that enabled abrupt glacial terminations do not exist today.

Glacial intervals were punctuated by multiple rapid events, the D-O cycles, which are characterized in Greenland ice-core records by a rapid increase in surface air temperature by 10 to 15°C over 10 to 200 years. These rapid warmings, examples of a tipping point being crossed repeatedly (28), were followed by slower coolings. D-O cycles have a global but spatially heterogeneous footprint (29, 30): Abrupt warming over much of the Northern Hemisphere was accompanied by cooling in much of the Southern Hemisphere (31) (**Figure 2**) (**Supplemental Figure 2**). The mechanisms behind D-O cycles are not fully established, although they are widely thought to be driven by spontaneous changes in the Atlantic Meridional Overturning Circulation (32, 33). Certainly, the mechanisms differ from those responsible for contemporary global climate change. However, the D-O warming phases show that large and rapid climate changes, of a magnitude comparable to that of expected changes in regional climate under future high-end projections, can happen—and have happened before hundreds of times (34).

Other short-lived climate events of smaller amplitude have occurred during the Holocene. Their occurrence during the Holocene is particularly important because they occurred under conditions closer to those of the preindustrial climate state. A cold event at 8.2 ka, which lasted for 150 to 200 years, was likely triggered by freshwater inputs into the Atlantic—although the exact mechanism is still debated (35). Nevertheless, it was global in extent (36) (**Supplemental Figure 3**). There is evidence for a similarly triggered cold event during the Last Interglacial (37). The so-called 4.2 ka drying event has been claimed as a major cause of change in human cultures (e.g., 38), but evidence that it was a global event is weak (36, 39) (**Supplemental Figure 3**). Even in the circum-Mediterranean region, where the signal is clearest, many records do not show the event (40). This event has been attributed to changes in solar irradiance or volcanicity, but it could equally be a manifestation of internal (unforced) climate variability. Observations of floods and droughts associated with the 4.2 ka event, albeit localized, may provide insights into the impacts of unforced climate variability in the future.

Reconstructions of past climates can be used to infer rates of climate change. An influential assessment of rates of change during abrupt events in the paleorecord suggested that they were

Mid-Pleistocene transition (MPT): a shift in the dominant climate periodicity from 41 to 100 ka between 1.25 and 0.7 Ma

Dansgaard–Oeschger (D-O) cycles: decadal- to centennial-scale climate warmings in Greenland, followed by slower (millennial-scale) cooling, that occurred 25 times during the last glacial

El Niño–Southern Oscillation (ENSO): a leading mode of climate variability on subdecadal timescales caused by oceanic and atmospheric circulation changes in the tropical Pacific

Paleocene–Eocene Thermal Maximum (PETM): an ∼200 kyr interval starting with 5–8°C global warming, ∼55.8 million years (Ma) ago

Pliocene: a warmer-than-present interval between 5.33 and 2.58 Ma, during which the progenitors of modern humans appeared

Last Glacial Maximum (LGM): coldest period during the last glacial when continental ice sheets were most extensive and sea level was lowest (∼22 ka)

Supplemental Material >

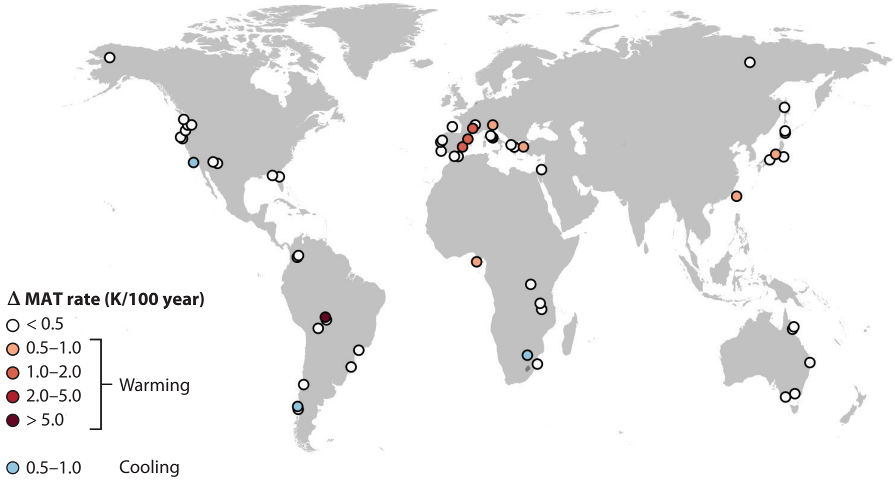

Figure 2

Site-based reconstructions of median rate of change [degrees Kelvin (K) per 100 years] in mean annual temperature (MAT) across the eight Dansgaard–Oeschger (D-O) warming events identified in Greenland during Marine Isotope Stage 3 (MIS3, 57 ka to 29 ka). D-O warming events in Greenland were expressed as both warming (*red dots*) and cooling (*blue dots*) in other regions; therefore, the plots show the absolute rate of change in K. Note that the registered cooling is small (0.5–1.0 K) compared to the registered warming (which can be >5 K). **Supplemental Figure 2** shows the reconstructed changes in summer and winter temperatures for comparison.

Supplemental Material >

orders of magnitude slower than those projected by climate models for the twenty-first century (41). However, this assessment is misleading. First, temperature changes associated with the end glacial and last deglaciation warmings were assessed to have taken place over very long periods (around 10 kyr and 2 kyr, respectively), based mainly on marine records—but this assessment is inconsistent with evidence for abrupt warming taking place over only a few decades, as shown in Greenland ice core records and in Europe (42), and with the Greenland ice-core record of CH_4, which has sources widely distributed across the continents. Second, D-O cycles were entirely neglected. We conclude that the rate of contemporary climate change is unusual but (in terms of regional climates) not unprecedented, suggesting that closer study of past rapid climate changes could provide useful information about the present and future (**Figure 2**).

Paleoenvironmental data and paleoclimate reconstructions provide a comprehensive picture of the geographic patterns of climate changes in response to global forcing, particularly for intervals during the late Quaternary. The largest geographic patterns of climate change between the LGM and Holocene, and during the Holocene, are now well-established. They include changes in monsoon strength and extent, an amplification of temperature changes in high northern latitudes versus lower latitudes (polar amplification), and stronger temperature responses over land than ocean (land–sea contrast). The last two phenomena are reproduced correctly by climate models (43, 44). Models also show orbitally forced monsoon expansions, in both the current and the previous (Eemian) interglacial, but they are systematically underestimated (43, 45–47). Other features of the last glacial and mid-Holocene climates are poorly captured by most or all current climate models. These features include a general failure to simulate a cool mid-Holocene in the Mediterranean region (45) and a tendency toward excessive simulated mid-Holocene drying in central

Eemian: the Last Interglacial (130 ka to 115 ka); warmer than the Holocene in the northern extratropics

Eurasia (48) (**Supplemental Figure 4**). These analyses urge caution in interpreting modeled regional patterns of future climate change. Although mapping of geographic patterns of climate change for earlier periods is limited, it has been done for D-O events (29) and, to some extent, for the Eemian (49, 50).

Supplemental Material >

Little Ice Age (LIA): period of quasi-global cooling in the thirteenth through nineteenth centuries, caused by multiple large volcanic eruptions and solar activity minima

3.4. Climate Variability Modes

The paleorecord provides evidence for changes in climate variability modes including the ENSO and the Atlantic Multidecadal Oscillation. ENSO variability has progressively strengthened since the mid-Holocene in the Pacific, driven by changes in insolation (51). However, present-day teleconnections associated with these modes of short-term variability are not static over time. For example, the orbitally driven decrease in monsoon strength over northern Africa and the Indian subcontinent during the last 6,000 years is associated with decreased interannual-to-decadal rainfall variability over northern Africa but increased interannual-to-decadal rainfall variability over India (52). Climate models have a limited ability to simulate past changes in variability modes (51, 52), casting doubt on their ability to represent future changes and teleconnections accurately.

3.5. Solar Variability and Volcanism

Paleodata have been used to investigate the role of volcanic events and changes in solar irradiance on climate variability. The HolVol database documents volcanic eruptions during the Holocene on the basis of sulfate and sulfur records from ice cores (53). Reconstructions of solar irradiance over much of the Holocene, based on concentrations of the cosmogenic isotopes ^{14}C and ^{10}Be in natural archives (54), are consistent with direct observations of sunspot numbers during the recent historic period. Climate variations have also been independently reconstructed from tree rings and other archives (55).

The Holocene was not, as often assumed, a period when long-term (multimillennial) changes were accompanied by stability in the shorter term. Instead, prolonged (decadal to centennial) cold phases during the Holocene were linked to clusters of volcanic events and phases of reduced solar irradiance. The four coldest phases during the Little Ice Age (LIA) have been linked to low solar irradiance (56), but other periods of low solar irradiance during the Holocene are not linked to cold events; in addition, model simulations, forced by reconstructed changes in solar irradiance and volcanism, suggest that volcanic events are more likely the main cause of prolonged cold intervals (57). Although the interactions between volcanic events and changes in solar irradiance and their combined influence on atmospheric circulation are not fully understood (58), we now at least have clarity about the causes of the LIA and about the approximate magnitudes of solar and volcanic effects, and we know that these effects cannot in any way explain the warming of the past 100 years (59), which is unequivocally anthropogenic.

4. ECOSYSTEM RESPONSES TO ENVIRONMENTAL CHANGE

Many of the phenomena discussed in Section 3 have been inferred from biological as well as geochemical evidence. Consensus among independent data sources strengthens the evidence for specific climate changes in the past, and biotic data can then provide additional information on how organisms and ecosystems have responded to changes in climate.

4.1. Responses of Plant Communities to Changes in Climate

Major climate changes have been accompanied by biome shifts, evidenced by large changes in pollen assemblages—from which it can be inferred that contemporary climate change will also cause biome shifts (60). A few long pollen records (see Section 2) document the responses of biomes to multiple glacial–interglacial cycles, providing evidence for changes in their duration and intensity. These records also reveal legacies from past vegetation that are relevant for understanding modern plant communities, such as remnants of subtropical floras in extant Mediterranean ecosystems (61). The persistence of many tree taxa in both temperate and tropical regions through multiple climatic cycles indicates considerable resilience to large changes in climate (62).

Over the past 10^5–10^6 years, taxa in many groups of organisms (including plants) have shown remarkably little macroevolution and few extinctions—despite Earth's climate being punctuated by multiple episodes of rapid change, accompanied by rapid biome shifts (29). The dearth of extinctions during repeated glacial–interglacial cycles, called the "Quaternary conundrum" (63), challenges our understanding of the responses of species distributions to climate change. For most groups of large organisms, including plants (64) and beetles (65), PNC has favored range shifts, rather than adaptive evolution, as the principal response to environmental change. Dawson et al. (64) noted four distinct modes of species response to large climate changes and provided examples of each among both plants and mammals. These modes are toleration (persistence in situ), habitat shifts (relocation to different microhabitats, observed especially in montane regions), migration (range shifts, sometimes over hundreds or thousands of kilometers), and extinction. To date, only one plant species (*Picea critchfieldii*), among hundreds of modern species identified from the last glacial period, is known to have suffered global extinction around the time of the last glacial termination (64). In contrast, regional extirpation of tree taxa has happened occasionally, leading (for example) to a gradual depauperation of European tree flora over multiple glacial–interglacial cycles (66) and the disappearance of some tree taxa (particularly gymnosperms) from large regions during periods of rapid climate change (67). It seems likely that plant species will show a comparable diversity of responses to rapid climate change in the future.

Mammals show a different pattern of response. Small mammals underwent genetic reorganization and suffered some extinctions (68). Many larger mammal species became globally extinct during the rapid warming phases of D-O cycles (69). Many more became extinct during the centuries after the last glacial termination. The extent of the human contribution to large mammal extinctions around the last glacial termination has been controversial for decades, and remains so (70, 71). However, earlier glacial terminations were also associated with large mammal extinctions, and genetic evidence points to both human and climatic influences on mammalian population sizes during the last glacial and Holocene periods (72). Some large herbivore extinctions have been linked to the transition from C_4 to C_3 vegetation dominance in many regions over the last glacial termination (73), an indirect effect of changes in CO_2 and climate. Paleodata thus indicate that, among different groups of organisms, large mammals may be the most—and trees among the least—vulnerable to rapid climate warming.

Settele et al. (74) considered spatial velocities of future climate change for regions of different topographic complexity under different scenarios. On the basis of modern observations, they estimated that the ability of large mammals to match these velocities was many times greater than that of trees. The paleoecological evidence directly contradicts this assumption. It suggests that without active conservation interventions, such as captive breeding and assisted migration, large mammals are at high risk of extinction from rapid warming. Many tree species may also be at risk of extinction today but for a different reason, namely continuing deforestation, especially in the species-rich tropics (75).

4.2. Rates and Mechanisms of Tree Species Migration

Past migrations of many tree species (**Figure 3**) have been several orders of magnitude faster than would be predicted on the basis of measured dispersal distances and maturation times, a

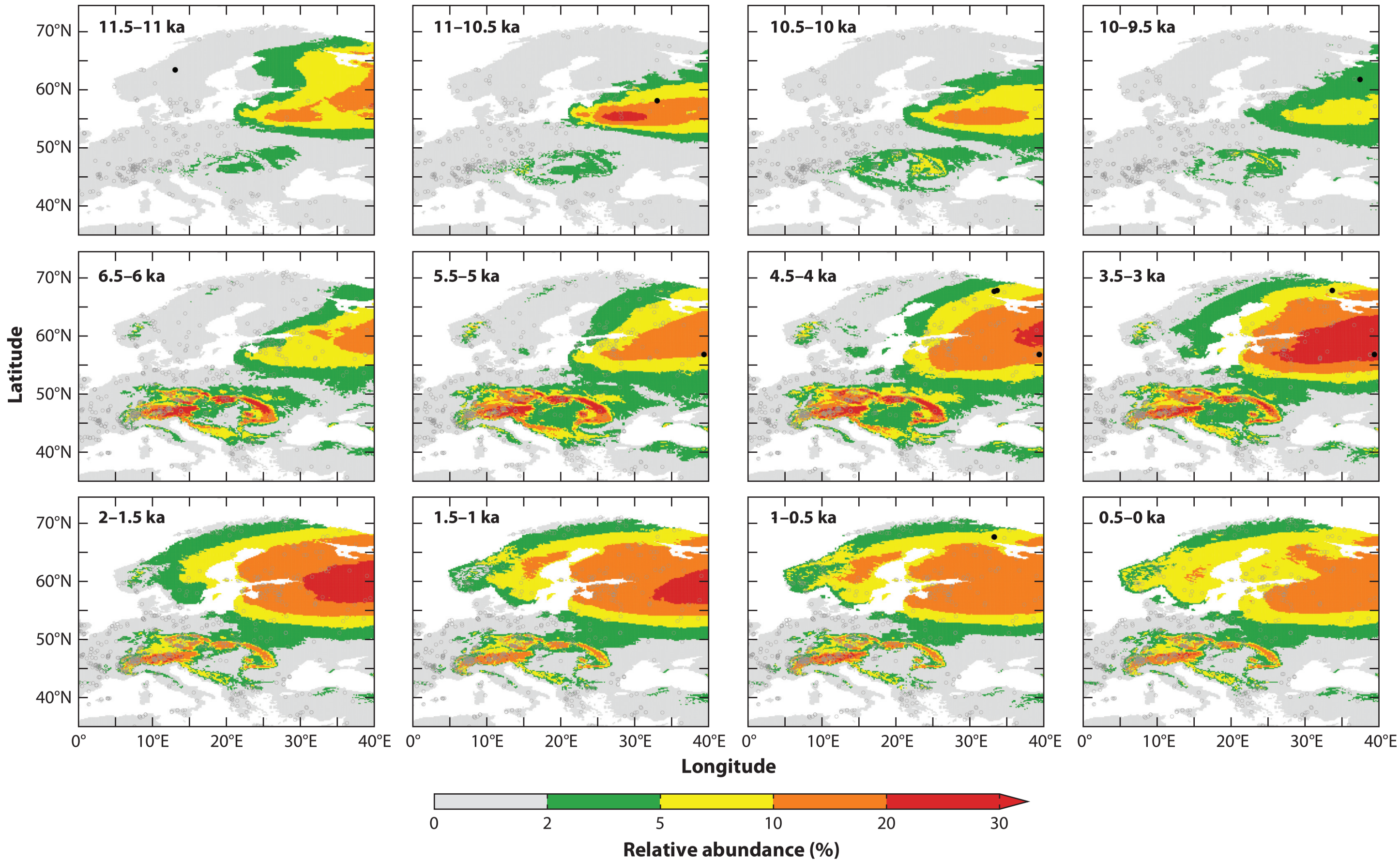

Figure 3

Relative abundance of *Picea* pollen across Europe in selected 500-year windows through the Holocene, interpolated from individual records using a thin-plate spline onto a 10-arcmin grid. Black dots represent the occurrence of *Picea* macrofossils. The pollen records show an initial phase of low abundance in the earliest Holocene followed by a rapid expansion into mountain regions in Southern Europe starting around 9.5 ka. A gradual expansion in northern Europe begins around 9.5 ka (kilo annum before present, where present is defined as 1950 CE), followed by a steady progression westward into Scandinavia that reaches maximum expression by approximately 2.5 ka and persists thereafter. Pollen records are from the SPECIAL-EPD (155), which provides standardized Bayesian age models using the INTCAL2020 radiocarbon calibration. *Picea* macrofossil data are from Reference 156.

phenomenon known as Reid's paradox (76). A possible explanation for this paradox is that, when climate change increases the favorable area for a tree species, occasional long-distance dispersal events found outlying colonies that then act as nuclei for infilling of a greatly expanded range (76, 77). This mechanism seems consistent with evidence that Holocene range expansions of some tree species seem to have proceeded by gradually increasing average abundances over a large area, rather than as a migrating front (78).

Reid's paradox: the observation that plant ranges shifted poleward after the LGM, orders of magnitude faster than observable seed dispersal distances allow

An alternative explanation for the apparently rapid migration of tree species invokes cryptic microrefugia (79), which could have provided nuclei for expansion when the climate changed. Evidence for some of these microrefugia is disputed, however (80). Microrefugia cannot, in any case, explain rapid migration into and across previously glaciated terrain. Post–glacial migration velocities of two wind-dispersed conifers, *Pinus banksiana* and *Picea mariana*, across formerly glaciated terrain ranged from 16 to 35 km/century (81). This rate is an order of magnitude faster than the tree migration rates inferred by Settele et al. (74). The earlier appearance of freshwater plants in northern Europe compared with land-dwelling plants in the early Holocene has long been attributed to slow migration of trees (82). Alternatively, it could reflect differences between aquatic and subaerial climates in a given location, with lake water temperatures responding differently from the surrounding land.

The ability of tree species to migrate rapidly probably depends on regional topography and species characteristics, in ways that are not fully understood. Prentice et al. (83) showed that changing distribution and abundance patterns of major tree taxa in eastern North America since the LGM could be explained by climate change—which would be possible only if species abundance patterns stayed close to equilibrium with climate. That study considered only intervals of 3,000 years and, thus, could not detect lags shorter than around 1,500 years. However, other studies have shown more rapid, centennial-scale adjustments to climate at regional scales (e.g., 84). Migration of some species in western North America was paced by a combination of intermittent dispersal events and occurrence of hydroclimatic windows suitable for populations establishment and expansion (85, 86). Multidecadal to multicentennial climate variability interacted with species' regeneration niches (generally narrower than adult niches) in governing colonization and subsequent backfilling (87). The situation in Europe appears to be more complex. Using a dynamic global vegetation model combined with a dispersal kernel, Zani et al. (88) compared simulated species distributions with and without dispersal limitation. They found that dispersal limitation was necessary to explain the late spread of some tree species during the Holocene.

All analyses of this kind are subject to uncertainties regarding the climate variables considered, how species' climatic niches are estimated, and the source of the climate data (modeled or reconstructed) used to create the simulations. If these methodological issues can be resolved, then the dense network of pollen data available from some regions (particularly North America, Europe and east Asia) should provide a unique source of evidence for the rate at which tree species' ranges can adjust to large changes in climate. This is currently one of the least certain processes for modeling future changes in terrestrial ecosystems.

4.3. Impacts of Rapid Climate Change on Community Composition and Biodiversity

Climate changes have had major impacts on community composition, biodiversity, and other ecosystem properties. Pervasive features of the paleorecord are the frequent appearance of "novel" communities and the disappearance of others. Nearly all extant plant communities have arisen since the LGM (60), and community turnover has been strongest during large and rapid climate changes. After the last glacial termination, wide areas of North America, Europe, and elsewhere supported plant communities that differed from modern plant communities in composition, with unique combinations of species and abundances and representing unique combinations of seasonal temperatures and precipitation (89). Although novel ecosystems are a controversial topic among conservationists, the paleoecological evidence is clear: Community composition has been, and will continue to be, transient. An obvious practical implication is that practical conservation in a fast-changing environment should build on nature's response to change, rather than perpetuating the idea of preserving species and communities in situ (90).

A worldwide acceleration of plant community turnover during the past 3 to 5 kyr has been quantified, on the basis of rate-of-change statistics, and attributed to human impacts (91). This explanation is not secure, however, because despite widespread pollen evidence for intensifying human impacts on ecosystems during the latter part of the Holocene (e.g., 92), this period was also far from stable climatically. Some regional case studies have indicated a lack of temporal correspondence between vegetation changes and the changes in human settlement and land use patterns to which they have been attributed (e.g., 93). The exact causes of Holocene vegetation changes across the world have not been established and require deeper investigation.

Sedimentary ancient DNA (sedaDNA) offers a new kind of information about changes in local plant communities by allowing the identification of a very much larger set of taxa (at species level) than can be achieved by pollen analysis (94). Research in Fennoscandia has indicated that total plant biodiversity generally increased throughout the Holocene (95), independently of climate change, even as functional plant-trait diversity reached a plateau around the beginning of the Holocene (96). This contrast suggests that ecosystem function is likely to be maintained in the face of a rapidly changing climate, while total floras may take several millennia to approach equilibrium with climate.

sedaDNA: fragments of genetic material (DNA) preserved in sediments and analyzed by high-throughput genome sequencing, used to identify the species present

Eocene: a warm climate interval between 56 and 33.9 Ma, characterized by extensive polar forests and a major expansion of mammals

4.4. Physiological Effects of Atmospheric CO_2 Concentration

Atmospheric CO_2 affects plant physiology: Increasing CO_2 increases the photosynthetic rates of C_3 plants (an effect which saturates) and decreases the water requirements for photosynthesis (which does not). The warm, ice-free Eocene world, with CO_2 levels exceeding 1,500 ppm, harbored forests at all latitudes (97). The LGM world, with CO_2 levels around 185 ppm (close to the all-time minimum), showed a greatly reduced forest area and widespread dominance of tropical vegetation by C_4 plants and temperate mid-latitudes by conifers. Climate and ecosystem models can simulate this world only if the physiological effect of low CO_2 is explicitly included (98, 99). Recognition of this direct CO_2 effect on plants has led to a reassessment of earlier reconstructions of dry conditions in glacial times. For example, the impact of low CO_2 during the last glacial period on plant growth explains why plant communities typical of relatively arid conditions today existed in environments where other lines of evidence, including the presence of lakes and large rivers, attest to wet conditions (100, 101).

"Woody thickening" (increasing tree cover in savannas) has been widely observed in recent decades (102). The observed impacts of past CO_2 changes suggest that it is caused, at least in part, by increasing CO_2 (103) and, therefore, that it will continue while CO_2 continues to rise. However, paleoecological evidence contradicts claims of a drying world due to rising CO_2 (e.g., 104). Such claims have been based on modeled increases in vapor pressure deficit (which reduce primary production by increasing stomatal closure) and aridity, measured by the ratio of potential evapotranspiration to precipitation. Both tend to increase globally as CO_2 rises. However, climate models do not simulate reduced primary production under enhanced CO_2 (105), and paleodata show strongly increased vegetation and tree cover in periods with high versus low CO_2. Drying trends due to anthropogenic climate changes are regional in extent, and other regions are experiencing increased rainfall (59).

4.5. Wildfire Regimes

Past vegetation disturbances, and changes in disturbance regimes, are documented in the paleorecord. Sedimentary charcoal provides evidence for changes in biomass burning (106). Biomass burning is a complex topic because wildfire occurrence is influenced by climate, vegetation, and human activities, which include habitat fragmentation (tending to reduce fire spread, but promoting fire in some ecosystems) as well as ignition and active fire management (107, 108). The extent to which past fire regime changes reflect changes in these various controls is controversial. Nonetheless, the paleorecord provides evidence for general principles that help to clarify the present situation.

First, low CO_2 reduced fuel loads, and therefore burning, in most regions during glacial periods (109). An example is provided by the regional dominance of *P. banksiana* in the unglaciated southeastern United States during the LGM. Today, this species is associated with frequent stand-replacing fires and shows specific adaptations to this fire regime, including serotinous cones. But LGM charcoal records show little fire in this region (110). It is likely that increasing CO_2 will contribute to increases in fire in some regions, through its effects on primary production (increasing fuel loads) as well as warming.

Second, paleodata support the existence of a peak in wildfire activity at intermediate precipitation levels—wet enough to support the production of copious fuel, but dry enough (at least during part of the year) to allow fuel to become dry enough to burn (106). Precipitation changes are expected to be regionally divergent, likely leading to increases in fire activity in some regions and decreases in others, depending on the direction of precipitation change and whether the current fire regime is limited by fuel or moisture.

Third, charcoal peaks are often associated with biome shifts—suggesting a mechanism by which climate changes can force rapid vegetation changes by increasing fire activity and thus hastening the transition toward more fire-tolerant vegetation (111). In today's climate, vegetation shifts are likely inevitable in regions experiencing large increases in fire activity (112).

In many populous regions today, most individual fires are ignited by human activities (whether accidental or intentional), leading to the assumption that biomass burning has increased in the twentieth century with increasing human population. This assumption overlooks the fact that total burned area is typically dominated by a small number of very large fires ignited by lightning. Charcoal records show that biomass burning in most regions was more extensive in preindustrial times than today and suggest that the subsequent decline was likely due to widespread suppression of burning by intensification of agriculture since the late nineteenth century (113). Climate model simulations that do not take this finding into account greatly underestimate preindustrial pyrogenic aerosol loadings (114). Projections of future fire risks need to account for the effect of human activities in suppressing as well as promoting fire.

4.6. Lessons for Conservation

Supplemental Material >

Knowledge of past ecosystem dynamics under environmental change informs biodiversity conservation, guiding action in a changing climate (115). Paleoecological studies provide baselines for the natural range of variability, determine key long-term processes responsible for ecosystem maintenance, and identify potential thresholds for ecosystem transformation (**Supplemental Table 4**). Paleoecology can help in assessing vulnerability of species populations (64) and ecosystems (116) to climate change. When ecosystems are threatened by climate-driven transformation in composition, structure, and function, ecological history can inform management responses by identifying when resistance is likely to fail and what alternative ecosystems might be sustainable under an altered climate (117). An important but often overlooked aspect of paleoecological knowledge

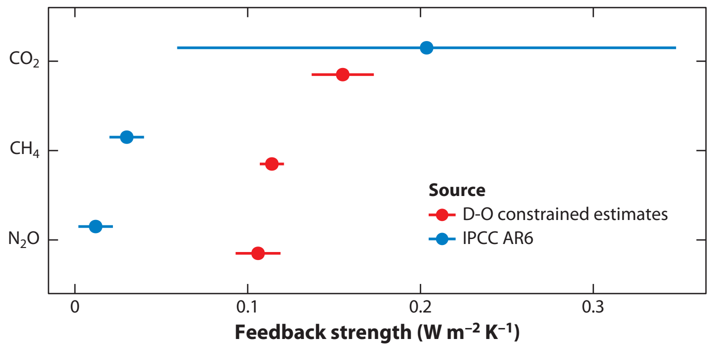

Figure 4

Estimates of feedback strength for carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), based on observed changes during the eight Dangaard–Oeschger (D-O) events that occurred during Marine Isotope Stage 3 (MIS3; 57–29 ka) (120), compared with the feedback strength as given by climate models used in the Intergovernmental Panel on Climate Change's Sixth Assessment Report (7). Circles show the mean values, and the bars indicate the uncertainty. D-O-based estimates of CH_4 and N_2O are much larger than shown by the models; the D-O-based estimate for CO_2 is within the range shown by the models but shows that both the low- and high-end model estimates of this feedback are unrealistic.

is its ability to help decision-makers and other stakeholders envision futures that are unlike recent or historical states, which can, in turn, provide potential options for intervention to direct climate-driven ecological transformation toward desirable outcomes.

5. BIOSPHERIC FEEDBACKS

The rates and magnitudes of the rapid warming phases of D-O cycles are comparable to projections under so-called high-end scenarios of climate change, even though the baseline climate, mechanisms, and geographic patterns were quite different (118). These events provide opportunities to quantify biogeochemical and biogeophysical feedbacks in the climate system (119). They confirm the existence of positive climate feedbacks due to natural emissions of CH_4 and N_2O (120) (**Figure 4**), whose sources are predominantly from terrestrial ecosystems. D-O-based estimates of their feedback strengths are several times larger than values given by the IPCC's Sixth Assessment Report (7) (the origins of those estimates are unclear) but are consistent with the modeled values for land-based N_2O feedback given by Xu-Ri et al. (121).

For CO_2, whose sources are both terrestrial and marine, the D-O estimated feedback is also positive (**Figure 4**) and within the range estimated by coupled climate–carbon cycle models, but it is smaller than estimates based on a single Holocene event, the LIA, which was associated with a short-lived reduction in CO_2. The D-O-based estimate is likely to be more reliable because of the small magnitude of the climate and CO_2 changes over the LIA, as well as disagreement between different ice cores over the exact magnitude of the CO_2 change at that time (122). The magnitudes of the D-O estimated feedbacks are similar for three gases, CO_2, CH_4, and N_2O. Thus, assessment of carbon budgets should consider the positive feedbacks due to CH_4 and N_2O, which are similar in importance to CO_2 feedback.

Paleorecords provide some evidence on the long-term response of terrestrial carbon storage to changes in CO_2 and climate. The change in terrestrial carbon storage between the LGM and the Holocene can be estimated from the $\delta^{13}C$ (i.e., the ratio of the two stable isotopes of carbon, ^{13}C and ^{15}) of seawater, which is reflected in the $\delta^{13}C$ of marine benthic foraminifera. This method yields global estimates of total land carbon storage that are around 300 PgC less at the LGM than at the Holocene. Coupled climate–land ecosystem models can reproduce a lowering of carbon storage at the LGM, but they persistently overestimate the reduction, often by a factor of around two. A possible explanation is that these model calculations do not allow for changes in the amount of inert carbon contained in permafrost (123), which was probably substantially greater at the LGM. If this explanation is correct, it would support the prediction that permafrost thawing will (albeit slowly) release additional carbon into the atmosphere over the coming centuries (124) as a long-term consequence of global warming.

CH_4 release from thawing permafrost (including shallow seabeds, such as the Siberian shelf) has been postulated as a tipping point hypothetically leading to a large and rapid future increase in global temperature (125). This scenario is not supported by paleodata from the Last Interglacial, when Arctic land temperatures were 4–5°C warmer than today (126) but no CH_4 spike occurred (127). However, paleodata do show a rapid increase in atmospheric N_2O after the last glacial termination, perhaps due to a rapid invigoration of the terrestrial nitrogen cycle resulting from increasing land temperatures (128).

Arneth et al. (119) showed rapid changes in biomass burning and atmospheric dust content, with burning increasing and dust decreasing, over the last glacial–interglacial cycle. Fire and dust produce more complicated radiative forcing effects than do well-mixed greenhouse gases, and their changes during D-O events have yet to be quantified in terms of climate feedbacks. However, the carbon cycle component of the feedback due to biomass burning has been quantified for the Common Era (up to preindustrial time) (129). This component arises because a greater frequency of burning corresponds to a reduced global terrestrial carbon store and, therefore, all else equal, an increase in atmospheric CO_2. The feedback is positive because warming tends to increase fire activity (129) and was large enough to constitute a substantial fraction of the total climate feedback associated with carbon cycling by the land biosphere. A separate analysis in the same study based on recent satellite-based data yielded a similar feedback strength but with large uncertainty, due to the short record and the complexity of modern human impacts on fire regimes.

Biogeophysical feedbacks arising from albedo changes—primarily at high latitudes, due to the higher albedo of snow-covered surfaces and low or sparse vegetation—are potentially large and are expected to have been largest during glacial times, when forest cover in high latitudes was much less than present. These albedo feedbacks may have been large enough to have contributed, alongside ocean- and sea-ice-based mechanisms, to the general climatic instability of the last glacial period. However, further research is needed on the role of system-wide feedbacks and the coupling of biogeochemical cycles in past climate changes, if we are to better understand the potential for climate "surprises" and the scope for mitigating them.

5. THE INTERPRETATION OF PALEODATA

The paleorecord is a rich source of information on the climate system, with many lessons for understanding contemporary climate change. Nonetheless, care must be taken to avoid potential pitfalls in interpretation.

Terrestrial paleoclimate data have been collected mainly by regional experts, whose assumptions and methods vary. Interpretations of data may change as a result of scientific advances; older interpretations may need reexamination in light of new knowledge. For example, it is now well-understood that the primary controls on the species composition of vegetation are summer and winter temperatures and moisture availability, which act through separate mechanisms and have differential effects on taxa (130). Distinguishing summer and winter changes is important, because orbitally induced changes in seasonality mean that they are likely to have different histories. Moisture index and precipitation reconstructions from plant assemblages should account for the effects of changing atmospheric CO_2 on plant water use efficiency (131).

The interpretation of geochemical and isotopic indicators must account for possible multiple controls. For example, ^{18}O in tropical speleothems is generally interpreted as a signal of changes in precipitation—but it can also be influenced by changes in water source, changes in the amount of precipitation recycling along the trajectory, and changes in precipitation seasonality (132). Temperature dependency of meteoric precipitation can also influence ^{18}O in temperate speleothems (133).

Although it may seem convenient for climate model evaluation, the conflation of data sources reflecting different properties of climate to yield a single measure, such as mean annual temperature (55), should be avoided (see discussions in 134, 135)—especially because seasonality changes have been fundamental in shaping past climates, through orbital variations, throughout Earth's history. Moreover, given that published interpretations may be inconsistent and/or obsolete, data syntheses should never be based on published conclusions alone. The primary data must be compiled, publicly available, and transparently interpreted so that reassessment is always possible.

The assignment of ages to past events is a key issue. Considerable attention has been paid to developing calibrations and Bayesian methods for age-model construction during the era for which ^{14}C dating is effective. Nevertheless, many published records are based on older calibrations and age-modeling approaches. In some cases, such inconsistencies have little impact on the timing of an event. In others, they can shift an event's apparent age by hundreds of years (**Figure 5**) (**Supplemental Figure 5**). Thus, it is important to quantify age uncertainty and to avoid assuming synchroneity of events without adequate statistical support.

Chronology issues are even more salient beyond the ^{14}C-dating interval. Research on earlier glacial terminations, for example, is usually based on marine records that have been "tuned" to orbital changes—precluding their use for examining orbital controls on terminations (136). In contrast, speleothems dated using the uranium–thorium method provide absolute chronologies for multiple terminations going back 0.5 Ma and beyond (137). The availability of multiple age-depth models, complementary methods of band counting, and archives that provide information on multiple climatic parameters (42) enable statistically robust determination of the sequences of events during glacial terminations (138).

Global data synthesis is essential if paleoclimate information is to be used to inform contemporary climate science. However, such a synthesis must be based on primary data, using well-defined and up-to-date methods for paleoenvironmental reconstruction and chronology. An increasing number of research databases (**Supplemental Table 1**) fulfill these requirements and form a strong basis for using paleoclimate data to inform climate science.

Radiocarbon (^{14}C) dating: method to determine ages of organic material from decay of ^{14}C fixed in photosynthesis, providing ages up to 50–60 ka

Uranium–thorium dating: technique used to date speleothems back to ∼500 ka, based on secular equilibrium between isotopes of thorium and uranium

Paleoclimate Modelling Intercomparison Project (PMIP): international activity coordinating climate model experiments to understand global responses to past changes in forcing and feedbacks

Supplemental Material >

6. CONFRONTING DATA AND MODELS

Science involves observations of phenomena, followed by tests of hypotheses that might explain them. Quantitative models enable hypothesis testing. The imperative of future prediction in climate science, however, has inverted this process. Models have been developed first, without considering their application to conditions different from present. Paleoclimate observations have been considered primarily as providing tests for models (46). There is no recipe for what to do when the models fail.

The Paleoclimate Modelling Intercomparison Project (PMIP) illustrates this difficulty. PMIP has evaluated state-of-the-art climate models through successive IPCC assessments (**Supplemental Table 5**). These analyses have highlighted the shortcomings of climate modeling, because models have shown a large spread, as well as persistent biases, when simulating past climates. For example, climate models have consistently underestimated the expansion of the Northern Hemisphere monsoon during peak interglacial conditions, and this bias has not improved over

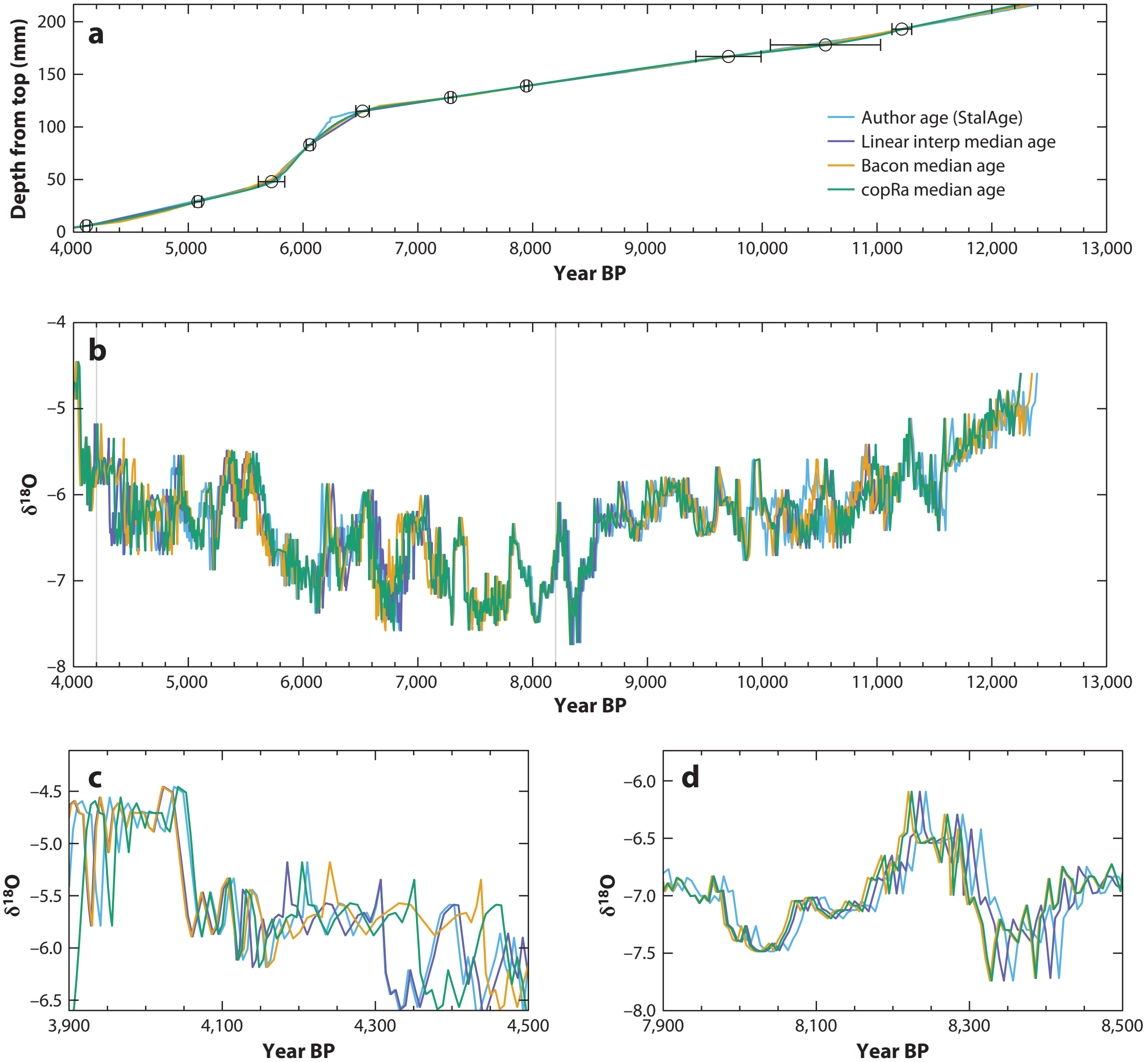

Figure 5

The potential impact of age-modeling uncertainty on the interpretation of paleorecords, illustrated using the record from the KM-A stalagmite from Mawmluh Cave, India. Plot *a* Uranium–thorium ages (as *circles*) and their uncertainties (as *bars*) along with a linear age-depth model constructed through the median of each age. Age is given in years before present (years BP), where present is defined as 1950 CE. Plot *b* Relationship between age and measured oxygen isotope content ($\delta^{18}O$) using multiple age-modeling approaches. Plots *c* and *d* show zoomed-in views of the 4.2 ka and 8.2 ka intervals. The different age models have little effect on the identification of the timing of the 8.2 ka event, but there is much greater temporal uncertainty for the 4.2 ka event depending on the age-modeling approach used. Figure based on data from version 3 of the Speleothem Isotopes Synthesis and AnaLysis (SISALv3) database (15).

successive generations. Biases from modern climate simulation often carry over to paleoclimate simulations (43, 44, 48, 139). Simulation of abrupt climate events has also proved problematic. Some models can produce abrupt climate changes, comparable to the rapid warmings associated with D-O cycles, when forced by freshwater inputs to the North Atlantic; however, they require unrealistically large inputs and cannot reproduce the sequence of events during the warmings (28).

We advocate a more traditional, hypothesis-testing approach to the use of climate models in paleoclimate research. A classic example is the demonstration (140) that the evolution of the African monsoon over the last glacial–interglacial cycle, as shown by the expansion and decline of large lakes in northern Africa, was a direct response to orbital forcing. Model experiments have also been used to test the importance of observed changes in land surface properties on climate (141). Comparisons with model simulations driven by known changes in orbital, ice-sheet, and greenhouse gas forcing have been used to explain differences in the temporal evolution of fire regimes between tropical and extratropical regions of the Northern and Southern Hemispheres over the last glacial–interglacial cycle (106).

The hypothesis-testing approach is powerful when used in model experiments to differentiate the potential influence of individual forcing mechanisms. Such experiments have been used to separate the impact of climate from the direct impacts of low CO_2 on productivity and water use efficiency in order to explain observed changes in vegetation and fire (98, 142) (**Figure 6**).

Fusion of paleoclimate data with models can help reconstruct past climates, especially when the number of reconstructions is limited. Data assimilation has been used in this way to assess LGM ocean (11) and land (143) climates. However, comparisons with reconstructions of global parameters that do not use model priors (44) suggest a need for caution when the spatial coverage of data points is uneven. Model simulations could be used more creatively to identify the likely trajectory of regional climate changes and thus, for example, to improve the identification of D-O events in paleorecords (31).

Perhaps the most useful way of combining data and models is to use paleodata as an integral part of model development (144, 145). Zhu et al. (145) used reconstructions of global cooling at the LGM to determine which of multiple different treatments of cloud microphysics was most realistic. In so doing, they showed that implementing the treatment identified as most realistic reduced the (extremely high) climate sensitivity of the standard version of the Community Earth System Model. Hopcroft et al. (144) used the mid-Holocene expansion of vegetation in northern Africa as a target to constrain uncertain parameters in the convection scheme in the Hadley Centre climate model, thereby improving the simulation of both mid-Holocene and present-day climates.

There will be a continued demand for paleodata for climate model evaluation, and it is imperative to improve existing data syntheses and the interpretation of these data. The examples mentioned above illustrate that observations of past climate states could also be used more creatively, both to test explicit hypotheses about the causes of climate changes and to improve existing models.

7. VADE MECUM

Earth system science would benefit from the mainstreaming of paleoclimate science as a source of (*a*) key challenges that models should address and (*b*) quantitative data describing features of climate change that models should be able to simulate but are not represented in the instrumental record. If models were better able to reproduce the diversity of climate changes that have taken place in the past, decision-makers would stand a better chance of avoiding being blindsided by surprises, as climate evolves toward states unlike those for which today's models were designed.

Biodiversity conservation is a major societal challenge, greatly compounded by climate change. Relevant observations are limited to the past century or so; thus, they provide very little information either about species and ecosystem responses to climate change or about processes that act on multicentennial to millennial timescales. These include the rates, patterns, and processes of species migration; interactions between climate variability and disturbance regimes; processes of community turnover; processes underlying major changes in vegetation composition and structure; and

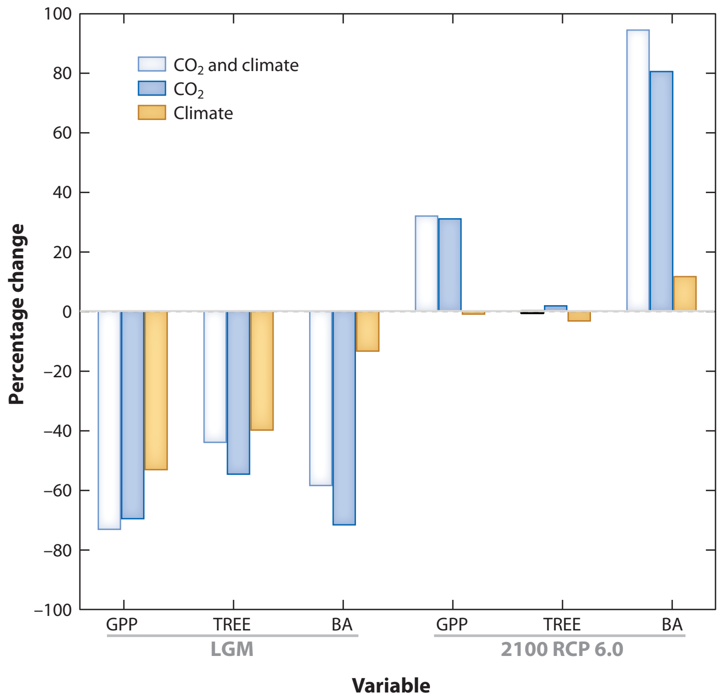

Figure 6

Example of the use of model experiments for hypothesis testing, showing realistic and counterfactual experiments to explore the impact of climate and CO_2 on vegetation and wildfires. Simulated percentage changes in gross primary production (GPP), tree cover (TREE), and burned area (BA) as a result of changes in climate, CO_2, and both climate and CO_2 at the Last Glacial Maximum (LGM) and by the end of the twenty-first century under the RCP (Representative Concentration Pathway) 6.0 scenario. The changes in GPP and tree cover were simulated using a light use efficiency model and the BIOME4 biogeography–biogeochemistry model. The changes in burned area were simulated using an empirical wildfire model that takes account of these climate and vegetation changes (108, 142). The graph shows the ensemble average results from multiple models for the LGM and RCP 6.0 (for plots showing the results of individual model simulations, see **Supplemental Figure 4**). Globally, GPP, tree cover and burned area are substantially reduced under the cold climates and low CO_2 of the LGM; the counterfactual experiments show that this effect arises predominantly from the low CO_2. Although changes in tree cover are small, both GPP and burned area are increased under the RCP 6.0 scenario; again, these changes are driven largely by the direct impact of CO_2. Accounting for both low CO_2 and a colder climate reduces wildfire activity at the LGM, but under the higher CO_2 and warmer climate of the RCP 6.0 scenario, the two effects amplify each other, leading to greater wildfire activity.

Supplemental Material >

gradual versus rapid transformations as well as their consequences for ecosystem function. Paleoecological data provide information about all of these processes, which should underlie conservation practice in a changing world.

The huge stores of information in paleoclimate archives are not being utilized to anything like their full capability. This review has showcased some of the contributions made by paleoclimate science to our understanding of contemporary climate change and its impacts. Much more can be learned, both from records we already have and from new paleoclimatic and paleoecological research that aims to acquire a fundamental understanding of what has happened in the past—and how and why.

SUMMARY POINTS

1. Data on past climates and ecosystems are obtained from many sources, both abiotic (geochemical, isotopic) and biotic (especially species assemblages). Ice cores contain indicators of global processes, including biospheric indicators such as CH_4 and N_2O.
2. Interpretation of species assemblages is aided by phylogenetic niche conservatism, which helps explain why species tend to migrate in response to rapid environmental changes.
3. Paleoclimate science has already contributed to contemporary climate science, for example, by constraining the equilibrium climate sensitivity.
4. Rapid (50–200 year) warmings during the last glacial period (Dansgaard–Oeschger events) and at glacial terminations provide information about the contrasting resilience of different organismal groups. For example, they demonstrate greater resilience for trees than for large mammals as well as the large magnitude of biogeochemical and biophysical feedbacks.
5. Natural wildfires have consistently been a pervasive force shaping plant communities.
6. Large contrasts in atmospheric CO_2, such as between the Eocene and the Last Glacial Maximum, attest to its key importance for ecosystem structure and function.
7. Conservation actions should be informed by the paleorecord, which documents the ubiquity of change (novel ecosystems are nothing new), and the variety of ways in which species respond to climate change, more effectively than analysis of contemporary data alone.

FUTURE ISSUES

1. Global synthesis of terrestrial paleodata should be accelerated—but with care, with regard to chronology, transparency, and the choice of variables to reconstruct. In particular, biotic assemblages should not be reduced to mean annual temperature.
2. Paleodata should be mainstreamed into climate science, where they could catalyze improvements to climate models, if creatively used.
3. Some long-standing discrepancies between climate model predictions and paleodata urgently require resolution.
4. Key information on the responses of ecosystem composition, structure, and function to environmental change will increasingly be obtained by exploiting the complementarity of different data sources, including sedimentary ancient DNA.
5. The roles of human and climate change influences on ecosystems during the Holocene, especially the past 3 kyr, remain muddled. Disentangling them will require explicit hypothesis testing and rigorous data analysis.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

AUTHOR CONTRIBUTIONS

S.P.H. and I.C.P. conceptualized the review and coordinated the discussions that defined the contents. P.J.B., E.C.-S., O.H., S.T.J., N.K., M.L., and D.T.R. designed and produced figures with input from all authors. S.P.H. and I.C.P. created the first draft of the article. All authors contributed to discussions, writing, and review of the article.

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