REVIEW SUMMARY

Using paleo-archives to safeguard biodiversity under climate change

Damien A. Fordham*, Stephen T. Jackson, Stuart C. Brown, Brian Huntley, Barry W. Brook, Dorthe Dahl-Jensen, M. Thomas P. Gilbert, Bette L. Otto-Bliesner, Anders Svensson, Spyros Theodoridis, Janet M. Wilmshurst, Jessie C. Buettel, Elisabetta Canteri, Matthew McDowell, Ludovic Orlando, July A. Pilowsky, Carsten Rahbek, David Nogues-Bravo
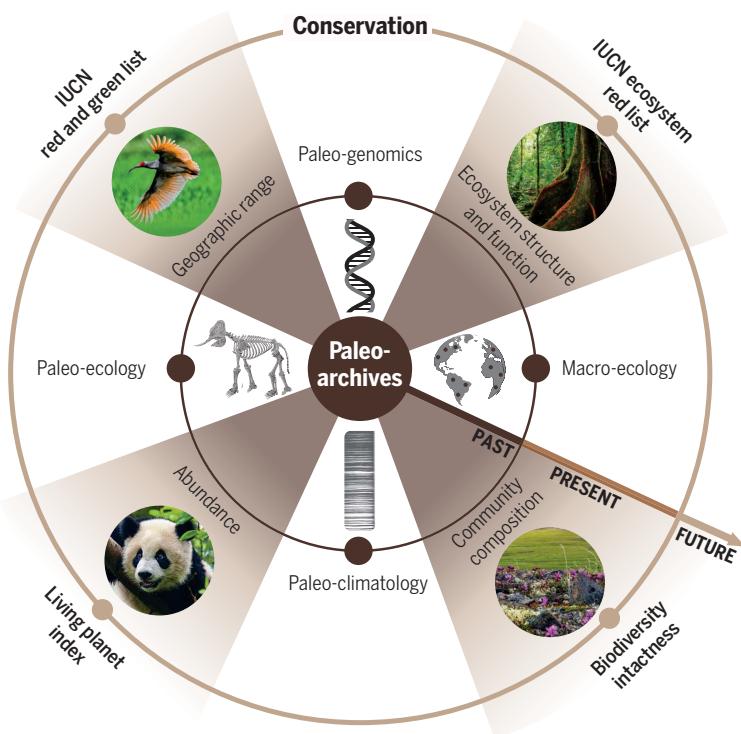
BACKGROUND: Effects of recent global warming have been documented in every biome on Earth. Safeguarding biodiversity and ecosystem services against future impacts requires reliable predictions of climate-driven biological responses and effective solutions. Integrated research in paleoecology, paleogenomics, paleoclimatology, and macroecology offers new prospects for projecting and managing current biotic responses to climate change. By revealing mechanisms that shaped past and present biodiversity patterns, this interdisciplinary intersection provides an empirical foundation for anticipating responses to accelerated climate change. New insights are coming from developments in high-throughput sequencing, computational technologies, ecological simulation models, and increased spatiotemporal resolution of paleoenvironmental data from late Quaternary paleo-records (the past ~130,000 years). Although these advances reveal biodiversity responses to past global change, benefits for improving forecasting of biodiversity impacts and refining conservation policies are lagging. Abundant opportunities exist for using the late Quaternary paleo-record to inform conservation practices and policies in the context of climate change.

ADVANCES: The threat of anthropogenic climate change demands that conservationists seek more effective ways of improving management of biodiversity and ecosystems. Analytical approaches that combine high-resolution paleoclimate proxy and simulation data, precisely dated fossils, and genetic diversity estimates from ancient DNA are unveiling biotic responses to various rates and magnitudes of natural climate warming, some comparable with 21st century projections. Reference periods in Earth's history provide natural laboratories for testing fundamental ecological theory and offer opportunities to identify ecological processes that influence the likelihood of extinction and ecosystem change, to test efficacy of threatened-species assessments and resilience of biota during periods of abrupt warming, and to locate biogeographic areas that remain stable under shifting climates. Refinement of essential biodiversity variables by using past biodiversity dynamics will improve our understanding of climate-driven shifts in species populations, community composition, and ecosystem structure and function. From this, biodiversity early-warning systems, conservation strategies, and decision-making tools can be tested at fine-grain spatiotemporal scales, providing an evidence base for understanding and improving projections of species- and ecosystem-level collapse.

OUTLOOK: As paleo-archives become more routinely integrated into conservation science, guidelines for the management of nature will benefit from understanding how different spatiotemporal scales of past climate change affected species and ecosystems across the planet. This will require global initiatives to harmonize vast numbers of paleoclimate-proxy and paleoecological records with high-resolution paleoclimate projections from Earth system models. Paleoecological data offer a means to disentangle climate and nonclimate drivers of biodiversity and ecosystem function, particularly in concert with simulation models and integrated analytical techniques that compare biotic change across regions with contrasting histories of human colonization and land use. Moreover, developments in paleogenomics that pinpoint adaptation across and within species will identify microevolutionary processes that lend resilience to biodiversity in shifting climates. Incorporating paleo-archives in conservation policies will equip decision-makers with improved strategies for mitigating biodiversity loss from climate change in the Anthropocene. ∎

Paleo-archives offer new prospects for benchmarking and maintaining future biodiversity. Integrated research using paleo-archives provides empirical foundations for contextualizing climate-driven changes in species populations, community composition, and ecosystem structure and function. These observations can inform conservation strategies under anthropogenic climate change.

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REVIEW

PALEOECOLOGY

Using paleo-archives to safeguard biodiversity under climate change

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Strategies for 21st-century environmental management and conservation under global change require a strong understanding of the biological mechanisms that mediate responses to climate- and human-driven change to successfully mitigate range contractions, extinctions, and the degradation of ecosystem services. Biodiversity responses to past rapid warming events can be followed in situ and over extended periods, using cross-disciplinary approaches that provide cost-effective and scalable information for species' conservation and the maintenance of resilient ecosystems in many bioregions. Beyond the intrinsic knowledge gain such integrative research will increasingly provide the context, tools, and relevant case studies to assist in mitigating climate-driven biodiversity losses in the 21st century and beyond.

Global mean temperatures are nearing the upper bound of those experienced over the past 1.2 million years ([1]), and their effects are being documented across every biome on Earth ([2]). As climate change intensifies in the coming decades, safeguarding biodiversity and the services that ecosystems provide to nature and people must remain high on the international policy agenda ([1]–[5]). Effective interventions will require conservation actions based on reliable predictions and evidence-based solutions ([3]). However, robust forecasts of species- to ecosystem-level responses to changing climates remain difficult ([4]), adversely affecting conservation planning and outcomes ([5]).

Research at the intersection of paleoecology, paleoclimatology, paleogenomics, macroecology, and conservation biology is offering new approaches to anticipate and manage responses of biodiversity and ecosystems to climate and other environmental change ([6]). By revealing ecological and evolutionary mechanisms that have shaped past and current-day biodiversity patterns, this research provides an empirical foundation for quantifying the broad footprint of accelerated rates of climate change on natural systems and for identifying long-term ecological and evolutionary processes that govern climate-biodiversity dynamics ([7]).

Although human land use, over-exploitation, and movement of non-native species remain primary drivers of biodiversity loss ([8]), climate change will grow in importance in the coming decades ([1], [9]). Paleo-archives allow biodiversity responses to climate perturbations of varying rates and magnitude, some approximating those predicted for the near future ([10]), to be tracked in situ (places where they occurred) over centuries to many millennia ([11], [12]). Past warming intervals provide critical reference points in Earth's history that can be used as natural laboratories to identify biotic vulnerability and resilience to rapid climatic change ([7]) and to connect ecological and evolutionary theory to the design and implementation of conservation practices to protect biodiversity ([13]).

Many species on Earth today have existed for hundreds of thousands to millions of years ([14]), having experienced many global glacial-interglacial cycles, each including rapid regional warming events, some spanning only decades ([15]). Although in many biogeographic regions these events are comparable in pace and magnitude with 21st century forecasts ([16]), they do not offer a direct analog for future global warming from recent anthropogenic climate forcing ([17]). Nevertheless, they can reveal actual species- and ecosystem-level responses to previous rapid changes in climate ([11], [12], [18], [19]). One of the most powerful features of the paleo record is its heuristic nature ([20]), providing concrete narratives, scenarios, and other thinking tools to better anticipate and visualize the potential ecological and evolutionary consequences of future climate change, enhancing knowledge of principles and mechanisms for conserving biodiversity and ecosystem services ([6], [7]).

Increased availability of precisely dated fossil records, genome-scale ancient DNA, and simulations with sufficient temporal resolution for reconstructing rapid climate change events means that the late Quaternary (last ~130,000 years) is providing new and effective opportunities to understand better the effects of climate change on biodiversity dynamics ([7], [21]), bolstering conservation knowledge ([22], [23]), particularly in the face of uncertainties on impacts of future climate change ([24]). This includes improved information on the mechanisms by which species have coped with high rates and magnitudes of climate change at a range of spatiotemporal scales, including those directly relevant to vulnerability assessments ([3]), based on sensitivities and adaptive capacities to climate change at human-relevant time scales ([5]).

With a growing emphasis on integrating paleobiology into conservation biology ([13], [20], [22]–[25]), and the emergence of conservation paleobiology ([6]), clear guidelines are needed to define when, where, and how scientists can use the late Quaternary paleo-record, spanning the 132,000 years since the start of the Last Interglacial (LIG), to provide insights for conservation policies that address climate change. The late Quaternary represents the origins of extant ecosystems ([21]), providing a suitable geohistorical period for informing responsible management of Earth's ecosystems and diverse biota under trajectories of future climate change. Here, we pinpoint where and when climatic transitions on human-relevant time scales are found in the paleoclimate record and show how these reference points in Earth's history can be used as mensurative experiments to establish likely consequences of future global warming for terrestrial biodiversity loss and ecosystem properties, including goods and services provided to humanity.

Approximately 40% of terrestrial ecosystems are projected to have experienced past shifts in temperature that are similar in pace and magnitude to regional-scale future forecasts ([16]). Thus, there is enormous potential to use geohistorical data to better derive and strengthen

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conservation management and policy through improved knowledge of biotic responses to climatic stressors. Leveraging these paleo "logbooks" of climate-driven biodiversity dynamics requires harmonized measures of ancient, recent, and forecast responses of biodiversity to climatic change. Newly constructed "essential biodiversity variables" (26) can quantify biotic change, vulnerability, and resilience to climatic shifts of the late Quaternary, as well as those in recent history.

Ancient warm periods and biodiversity consequences

Earth has both globally and locally experienced conditions warmer than the 20th century during the Quaternary and the Tertiary (10), providing numerous glimpses of what a warmer world looks like ecologically (27). Although not direct analogs for an enhanced-greenhouse future, because of different processes in the climate system (17), these ancient warm periods provide an empirical basis for identifying and understanding ecological and biogeographical implications of a warmer world, at spatiotemporal scales and levels of biological complexity that cannot be captured through deliberate experiments or direct monitoring.

Late Quaternary intervals comparable with near-future climate projections include the Holocene Thermal Maximum (HTM) between 12,000 and 5,000 years B.P. (before the present) (28, 29), in which surface-temperature anomalies relative to preindustrial climates were in some regions +3°C or more (Fig. 1), and the earliest millennia of the LIG (129,000 to 111,000 years B.P.), when the global mean temperature anomaly was >1°C above preindustrial conditions (10). Summer warming was prominent in Northern Hemisphere continental interiors during these periods; by contrast, ocean warming was comparatively small (Fig. 1). Deeper-time warm intervals include the Early Eocene (~50 million years ago) and the Mid-Pliocene (3.3 million to 3.0 million years ago), when atmospheric CO_2 concentrations were greater or comparable with that of the present; mean annual surface temperatures were >10°C (Early Eocene) and ~3°C warmer (Mid-Pliocene) than preindustrial temperatures (10).

During the HTM, warmer temperatures and different moisture regimes led to climate-driven movements of biome boundaries and elevational shifts in montane vegetation belts. For example, the tundra-forest boundary shifted ~200 km northward in Central Siberia (30), whereas the prairie-forest boundary on the North American Great Plains shifted ~200 to 250 km eastward under increased aridity (31). Montane treelines were lower than today on islands in the Southern Ocean during HTM, owing to drier conditions under higher temperatures (29). In much of northern subtropical Africa, HTM climate was wetter (although

cooler) than today, largely because of higher summer temperatures in the northern Sahara (Fig. 1) leading monsoon rains to extend farther north, allowing many savanna plants (and riparian and wetland animals) to extend their ranges northward by ~400 to 500 km in what is today a desert (32). In the Central Andes (South America), warm and wet conditions during the HTM resulted in plants moving up to 1000 m downslope (33).

During the LIG, boreal forests extended north into Greenland (34), whereas the Sahara was largely occupied by savanna (35). In Europe, warmer temperatures allowed the hippopotamus (Hippopotamus amphibius) to expand its range as far north as Britain (36). The occurrence of giant tortoise Hesperotestudo (Geochelone) crassiscutata in the American Midwest in the LIG implies temperatures above freezing throughout the year (37). Mid-Pliocene warming
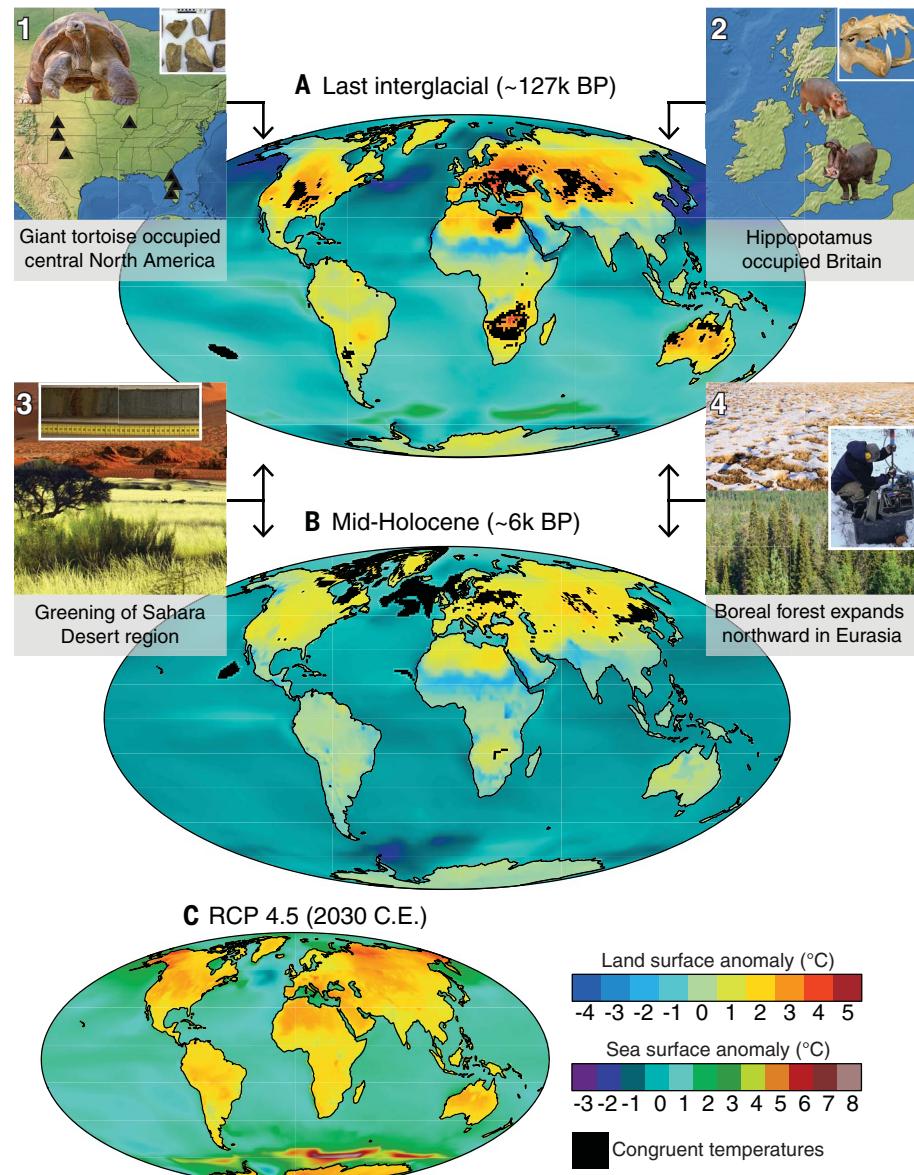
Fig. 1. Similarity in temperatures between past warm periods and the near future. (**A** to **C**) Boreal summer (JJA) land and sea-surface projected temperature changes from a preindustrial baseline for the (A) LIG (~127,000 years B.P.), (B) mid-Holocene (~6000 years B.P.), and (C) 2030 under RCP 4.5. Black areas in (A) and (B) represent locations with temperature anomalies that are congruent with (C). Boxes 1 to 4 show biotic responses inferred from paleo-archives (insets), with arrows pointing to the relevant time periods. Paleo-archives include fossil bones (boxes 1 and 2) and pollen in sediment cores (boxes 3 and 4). Triangles in box 1 indicate fossil sites. Paleoclimate simulations are detailed in appendix S1. [Image credits: Susan Schmitz, Smithsonian, Vincent Gordano Photo, Wlad74, Anan Kwaewkhammul, Janelle Lugge, JaySi, Northwestern, Real Window Creative, Natalia Golubnycha, Audrius Merfeldas]

caused similar latitudinal displacements in vegetation, including poleward contractions of tundra, northward expansions of boreal forest, and greening of the Sahara (*38*). Tundra-like communities with dwarf-shrub species of southern beech (*Nothofagus beardmorensis*) occurred at high altitudes in Antarctica (*39*), where today there is polar desert.

Well-documented geographic displacements of species and biomes across the globe during these past warm periods underscore the need for species' ability to shift their range boundaries by hundreds to thousands of kilometers in response to future warming. They also lead to expectations that many species will respond individualistically to future climatic changes, resulting in communities and ecosystems without modern analog (*40*). These mechanisms of biodiversity and ecosystem change are unlikely to differ, at least qualitatively, in the future (*41*).

Ecological ramifications of rapid warming

Between 21,000 and 18,000 years B.P., Earth began to emerge from a glacial climate—with low CO_2 concentrations, lower sea levels, and large land-based ice sheets—into the Holocene interglacial (*42*). During the global warming of the last deglaciation (LD; 20,000 to 10,000 years B.P.), many terrestrial regions experienced temperature increases of 4° to >10°C (Fig. 2). Some were gradual, but others occurred during episodes that spanned decades to centuries (*43*). In some regions, these rapid warmings were up to half as large as the entire difference between glacial and modern conditions (*44*).

Greenland ice cores reveal rapid large-magnitude warming events at 14,700 and 11,700 years B.P., with warming rates of ~10°C spanning decades (*43*). These are similar to rates forecast for Northern Hemisphere polar regions under Representative Concentration Pathway (RCP) 8.5 (Fig. 2). In Europe, regional temperatures increased 3° to 5°C during the rapid warming event 14,700 years B.P. (*45*). Although regional climates over the North Atlantic region and Europe reorganized quickly during the LD warmings, signatures of these rapid events are found globally at varying amplitudes and lags, including in the tropics (Fig. 2). In the southern hemisphere, more gradual and less pronounced warming events occurred during cold stadial periods in the northern hemisphere (*44*).

Paleoclimate simulations since 21,000 years B.P. suggest that 39% of terrestrial Earth experienced near-centennial climate shifts of similar magnitude to those of regional-scale future forecasts under RCP 8.5 (Fig. 3). These rapid temperature changes occurred largely during the LD (*16*). Zoogeographic regions (*46*) with the largest overlap between past and future paces of temperature change include Arctico-Siberian, Eurasian, Amazonian, and Novozelandic (Fig. 3); many of these regions are rich in paleoeco-logical records, providing natural laboratories for better anticipating biotic responses to climatic changes.

Past rapid warmings profoundly affected biological diversity at multiple levels, including genetic diversity, species abundances and geographical ranges, community composition, and ecosystem structure. In Eurasia, many cold-adapted mammal species experienced reductions in population size of 50 to 90%, causing bottlenecks and consequent losses of genetic diversity (*47*). Population decreases and extirpations were widespread in Eurasia and North America during the LD warming events, with accompanying shifts in species distributions (including that of anatomically modern humans) and reorganization of diversity patterns (*11*). For example, in Eurasia, the saiga antelope (*Saiga tatarica*) retracted its range, surviving the 14,700 years B.P. warming event in temporary cool refugia (*48*), whereas the Arctic Fox (*Alopex lagopus*) was unable to track habitat shifts associated with LD warming events in mid-latitude Europe, leading to regional extinction (*49*). In North America, species evenness of small-mammal communities decreased sharply in response to rapid warming, negatively affecting functional stability and community persistence (*50*), and a widespread and regionally abundant tree species (*Picea critchfieldii*) went extinct (*51*).

These alterations in species distributions and abundances radically changed the structure and function of ecosystems, influencing the physical formation of habitats, geochemical cycles, and primary productivity (*18*, *52*). For example, in Britain and Ireland, rapid warming caused changes in plant-soil and plant-plant interactions, resulting in above- and belowground shifts in ecosystem composition and overall reductions in productivity (*19*). Moreover, decreases in the ranges and abundances of terrestrial megafauna reduced their contribution to nutrient cycling and redistribution (*52*), with consequences for structure and function of ecosystems (*53*). Late-glacial population decline of megaherbivores in the North American interior reduced browsing pressure on broadleaved trees, provoking a rapid transition from coniferous forest to mixed coniferous-deciduous forest, along with a change in fire regime (*18*).

Geohistorical records of biotic responses to rapid warming events of the LD indicate that abrupt climate-driven changes in species distributions and numbers will be far reaching, causing feedbacks on the climate system (such as decreasing albedo and changes in evapotranspiration) that alter the pace of warming (*45*), affecting human well-being through changed ecosystem health and services (*54*). Because many LD warming events are similar in magnitude and pace to 21st-century forecasts (Figs. 2 and 3), LD paleo-archives provide invaluable "logbooks" for establishing how future global warming is likely to redistribute terrestrial biodiversity and change ecosystem functioning.

Biotic responses to extreme climatic events

Conservation management and planning decisions are typically based on species, populations, or ecosystems in specific habitats and locales, involving time horizons of seasons to decades. Paleo-archives offer opportunities, particularly in the mid- to late Holocene, to identify processes underlying climate-change responses at the taxonomic, spatial, and temporal scales used by decision-makers. Genetic and demographic studies of extant populations can often be tied seamlessly to late Holocene records of population and biogeographic dynamics accompanied by independent paleoclimate records.

Holocene paleoclimate reconstructions show that extreme climate anomalies are often clustered, resulting in periods of drought or high temperatures, with variable durations, return frequencies, and magnitudes (*55*). These episodic climatic events govern rates and patterns of range expansion and contraction (*12*). Studies of tree populations, for example, reveal the importance of nonstationary Holocene climate variability and its interactions with long-distance dispersal, local demographic processes, and species life-history traits (*56–59*). Moreover, Holocene records show that population expansions and declines are not necessarily accompanied by changes in geographic distribution (*60*, *61*), as is often assumed in conservation assessments (*62*). For example, a rapid population increase of eastern hemlock (*Tsuga canadensis*) near its western range margin was not accompanied by geographic expansion (*60*), whereas its geographic distribution held steady during a dramatic range-wide population decline (*61*). The latter example represents a rapid ecosystem transformation, in which a dominant conifer (hemlock) was replaced by deciduous trees and pines, forming forests with different structural and functional properties, in response to a contingent series of climatic and ecological processes operating at different temporal and spatial scales (*61*, *63*).

As threats of ecosystem transformations increase in response to current global warming (*64*), Holocene records offer opportunities to better understand the mechanisms that underlie these transformations. For example, paleoecological studies confirm that coniferous forest stands can be transformed by a single severe climate-driven fire event (*65*), a phenomenon that appears to be under way in parts of western North America (*66*).

Strengthening conservation policies and strategies

As anthropogenic climate change accelerates, the value of knowledge on past responses will
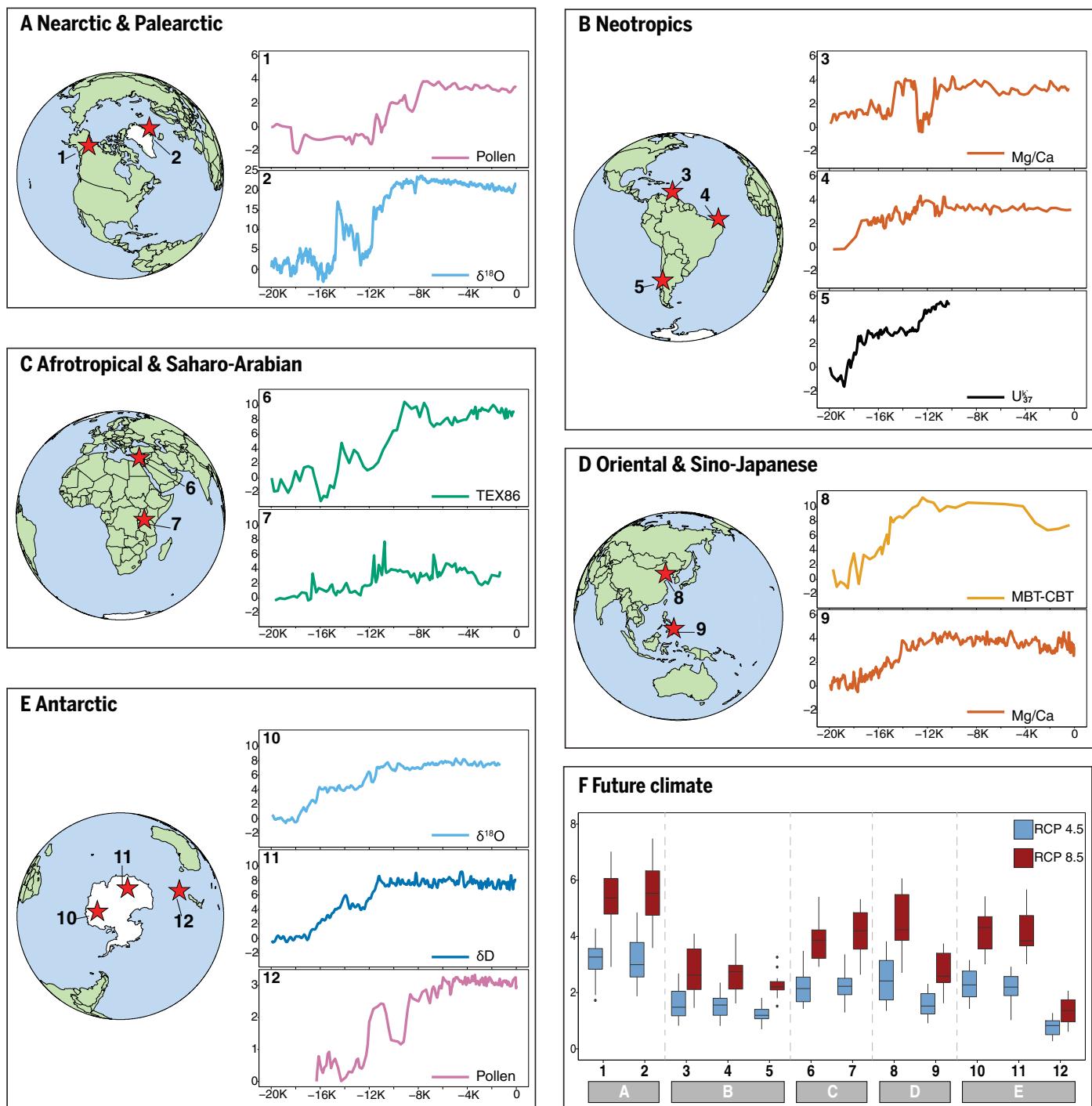
Fig. 2. Abrupt warming during the last deglaciation. (**A** to **E**) Temperature change (degrees Celsius; *y* axes) since 20,000 years B.P. (*x* axes) or the earliest record after 20,000 years ago [(A), 5; (C), 6; (D), 9; and (E), 12] for 12 paleoclimate reconstructions (*29, 99*) from eight zoogeographic realms (*46*), including Antarctica. (**F**) Boxplots show a multimodel averaged forecast of annual-mean temperature change for 2080 from a baseline focused on 1990 (*16*) under two radiative-forcing scenarios for sites in (A) to (E). The *y* axis scale differs in (A) to (F). The *x* axis shows time before the present in thousands of years. Details of paleoclimate reconstructions in (A) to (E) are provided in appendix S1.

depend on developing harmonized metrics that can be used reliably and consistently to quantify both past and recent trends in extirpation and extinction rates, community composition, and ecosystem structure and function (Fig. 4). In the modern context, ecologists have proposed classes of "essential biodiversity variables" (EBVs) for measuring biodiversity change and deriving conservation policies (*26*). However, to date, their temporal reach has been limited to a few decades (*67*).

Paleo-archives provide opportunities to estimate EBVs under a far wider range of shifts in climatic and environmental conditions, including variables measured at the population, species, community, and ecosystem levels (Fig. 4). The application of paleo-archives to a subset of EBVs (paleo-enabled EBVs) makes the direct translation of past biodiversity responses to future environmental management more straightforward because EBVs comprise
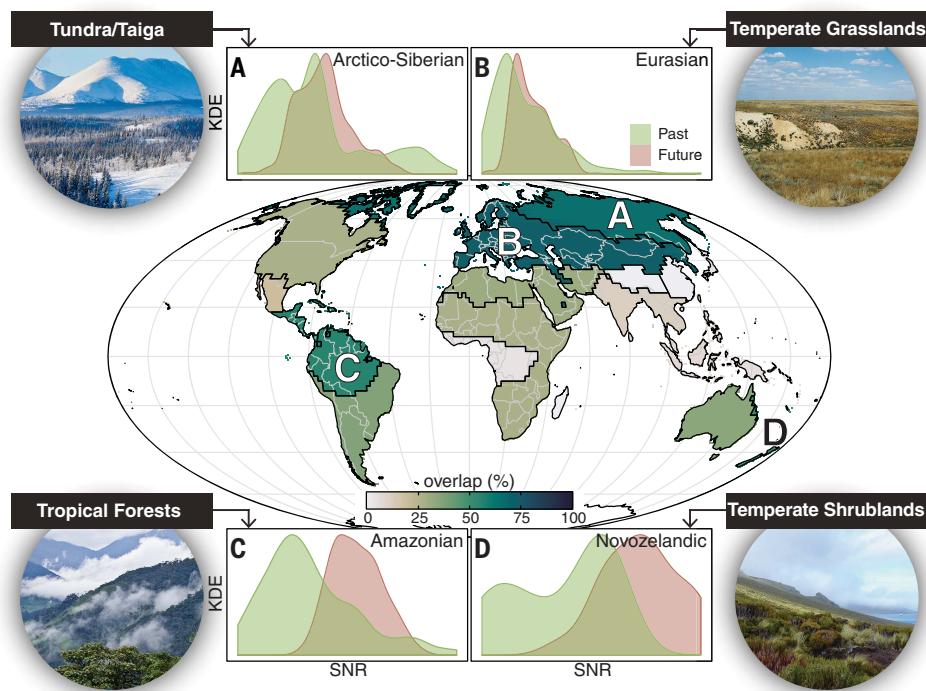
Fig. 3. Similarity in past and future rapid temperature shifts. Map shows overlap (%) in the signal-to-noise ratio (SNR) of rapid climate change events for past (21,000 years B.P. to 1850 CE) and future (21st century, RCP 8.5) temperature change in zoogeographic regions (46). Colors represent the percent overlap in SNR. (**A** to **D**) Plots show SNR distributional overlap (green indicates past, and red indicates future) within the (A) Arctico-Siberian (64%), (B) Eurasian (72%), (C) Amazonian (55%), and (D) Novozelandic (52%) regions based on kernal density estimates (KDE). Pictures show examples of ecosystems in regions (A) to (D) with geohistories suitable for assessing and maintaining future biodiversity. Data are based on (16). Distributional overlaps for all zoogeographic regions are provided in (100). [Image credits: Pi-Lens, Bogdan Kovenkin, Glenn R. Specht-grs photo, Dale Lorna Jacobsen]

a common currency for estimating and discussing biodiversity change among the scientific and policy communities (67).

Species distributions and abundances

Species' abundance is an EBV that can be inferred from fossil records (morphological, molecular, or both) by using count data or from genes in extant populations by using coalescent estimates of effective population size (Fig. 4). Probabilistic and bias-correction methods can be used to account for inconsistencies in radiometric dating, sampling rates, fossil preservation, and taphonomy (25, 68), making inferences of biotic change from paleo data more comparable with the abundance-based indicators of biodiversity change used today in conservation policy [Living Planet Index, International Union for Conservation of Nature (IUCN) Red List, and IUCN Green List], and assessment of biodiversity targets [Convention on Biological Diversity (CBD)] used in the face of anthropogenic climate and environmental change (69).

Because warning signals of biotic transitions or state shifts are commonly identified by using time-series abundance data (70), paleo-archives provide opportunities to test conservation criteria and model efficacy, improving knowledge of critical thresholds for population collapses,

possible extinction events, and ecosystem shifts (71). Moreover, a longer-term perspective enables natural variability bounds in species abundances and other conservation-relevant variables to be estimated over large-scale climatic shifts, often in settings where there were no substantial direct or indirect human impacts to confound the signal. In this way, paleo-archives allow thresholds of natural variability to be identified and integrated into threat-classification metrics to ensure that declines from greenhouse gas warming and other human-environment interactions are being prioritized (72).

Change in spatial distributions of species is another paleo-enabled EBV that can be inferred from the fossil record with ecological models and used to monitor single or aggregated taxonomic units under late Quaternary climate change, allowing improved understanding of natural distributions for recovery assessments and the role that climate had in past range contractions and expansions (Fig. 4, Muskox; *Ovibos moschatus*). Furthermore, paleo-enabled conservation variables allow morphological changes within species populations to be measured across time (Fig. 4) (22), providing a deeper understanding of species-level responses to climate change (73) and im-

proved capacity to detect ecological regime shifts (74).

Assessments of biodiversity values are strongly dependent on the spatial and temporal scale of their evaluation, which in turn influences conservation-planning decisions (22). The common method of using the historic record after 1500 CE as a baseline for vulnerability assessments (8) can overlook long-term trends in species ranges, population size, and genetic diversity (Fig. 4) (72). This can directly affect evaluations of conservation status (IUCN Red List) and measures of conservation success (IUCN Green List) (75). Although paleo-archives can address this shortfall, a challenge will be to develop and apply long-term comparative frameworks to biological signals preserved in paleo-archives for local and range-wide extinctions of related species and subspecies.

Paleo-archives are now being integrated into ecological and evolutionary models to improve theories and make generalizations regarding the spatial dynamics of range collapses of species (13). For example, a common view in conservation is that densities in peripheral populations are typically lower and less stable than at the center of a species' range (62), which has led to the widely adopted goal of avoiding the range periphery in conservation
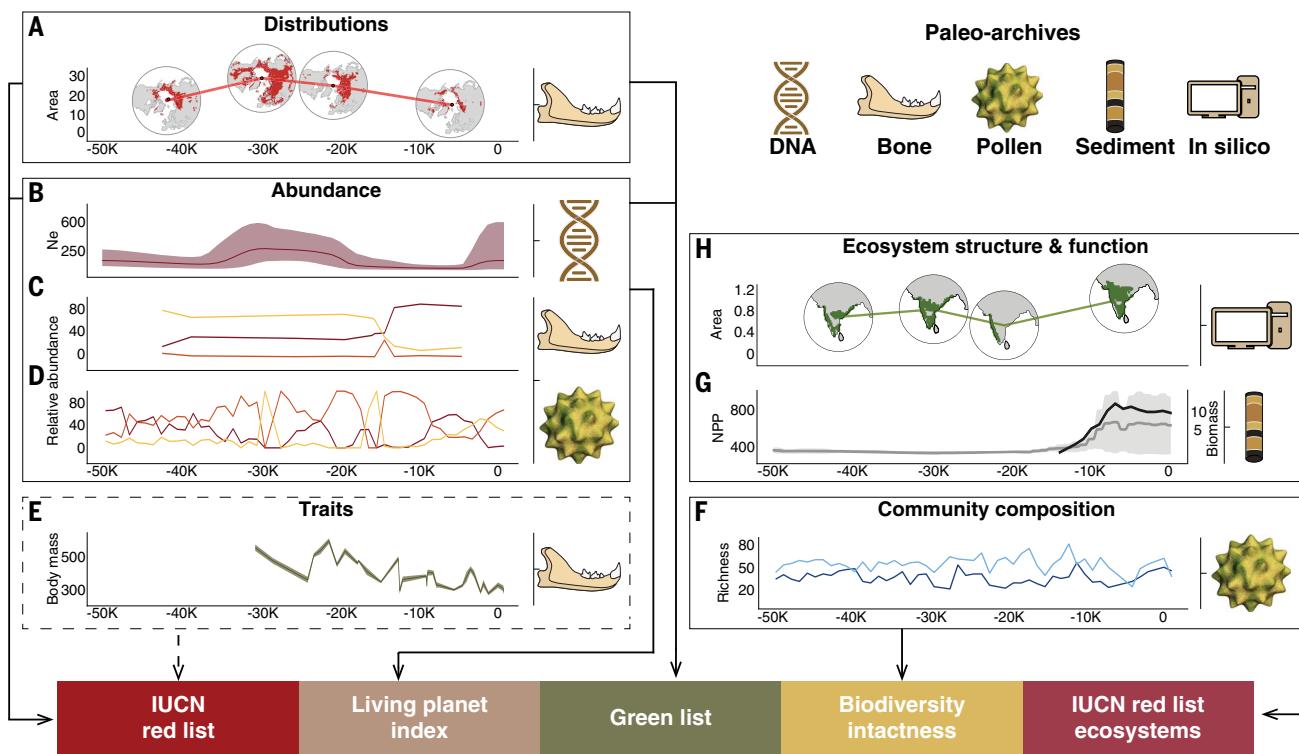
Fig. 4. Paleo-archives for informing conservation under climate change.
(**A** to **H**) Paleo-archives (DNA, fossils, and sediments, including in silico computational reconstructions) provide "log books" of changes in species' (A) distributions, [(B) to (D)] abundances, (E) traits, (F) community compositions, and [(G) and (H)] ecosystem structures and functions. Projected (A) geographic range (km^2 × 10^6) and (B) effective population size (N_e × 1000) of muskox (*Ovibos moschatus*); (C) Mammal relative abundance, southern Australia [*Pseudomys australis* (red), *Rattus fuscipes* (orange), and *Pseudomys apodemoides* (yellow)]; (D) Plant relative abundance, southern Italy [*Albies alba* (red), *Fagus sylvatica* (orange), and *Carpinus betulus* (yellow)]; (E) Woodrat (*Neotoma*

cinerea) body mass, Great Basin, United States; (F) Taxonomic richness of plants in southern Italy (dark blue) and Guatemala (light blue); (G) Net primary productivity, North America (gray), and plant biomass (black), eastern Canada; (H) Projected area (km^2 × 10^6) of savanna ecosystem, India. Relevant conservation schemes are the IUCN Red List, Living Planet Index, and IUCN Green List (abundance, distribution, and traits); biodiversity intactness (community composition); and IUCN Red List ecosystems (ecosystem structure and function). The x axis shows time before the present in thousands of years. Trajectories in (A) to (H) are detailed in appendix S1. [Image credits: LynxVector, Knorre, turtle_stock, flaticon]

strategies. However, if applied indiscriminately, this could result in extinctions of species whose persistence may depend on populations close to the periphery of their historical ranges (according to paleo-archives) (*76*). Inferences of range shifts during the late Quaternary offer distinct opportunities to develop an improved theory of population declines, allowing direct tests of the respective circumstances under which geographic ranges collapse first along the periphery or in the range interior.

Communities and ecosystems

The paleoecological record provides a wealth of data documenting properties of past communities and ecosystems and how they have changed at local to regional scales during the late Quaternary (*33, 54, 77*). Environmental DNA can (alongside fossils) document temporal dynamics of communities and ecosystems across hundreds to many thousands of years, helping to assess the resilience of ecosystem services to climate variation and change (*78*). Community reconstructions of taxonomic rich-

ness and evenness for plants and animals using paleo-archives (Fig. 4) can be used to calculate "biodiversity intactness" (*79*) and thus guide policies for reducing future biodiversity loss (*69*). This is done by quantifying change in the diversity of a wide assortment of organisms within a given geographical area after a climatic shift or other environmental disturbance. Furthermore, paleo-data can give insight into the relative roles of biotic and abiotic controls on ecosystem properties, including nutrient cycling (*19*), net primary productivity, and plant biomass (Fig. 4) over periods of stability and disturbance. These paleo-enabled measures of ecosystem function can reveal thresholds for ecosystem collapse and inform recent protocols for assessing ecosystem-level threat status under climate change (*80*).

Processes regulating climate-biodiversity dynamics

The challenge of synthesizing disparate evidence from paleo-archives—to assess threats to species and ecosystems from climatic change, and potential consequences of their loss—is

being addressed by using process-based (theory- and data-driven) simulation models. These approaches, which run at fine temporal and spatial scales and across large geographical extents, open windows into climate-biodiversity dynamics during the late Quaternary (*81*). By directly capturing spatiotemporal variations in biodiversity at biologically relevant spatiotemporal scales, simulation models provide improved ways to establish ecological baselines and to understand long-term ecological and evolutionary responses to climatic shifts and anthropogenic activities (*82*). They can be used to disentangle multiple drivers of biodiversity change and infer causality, making them particularly suited to guide decisions regarding the pace of change and desired states of ecological systems.

These process-based simulation models are increasingly useful for assessing the relative importance of ecological and evolutionary responses to different spatiotemporal scales of past climatic and environmental change in shaping different levels of biological organization.
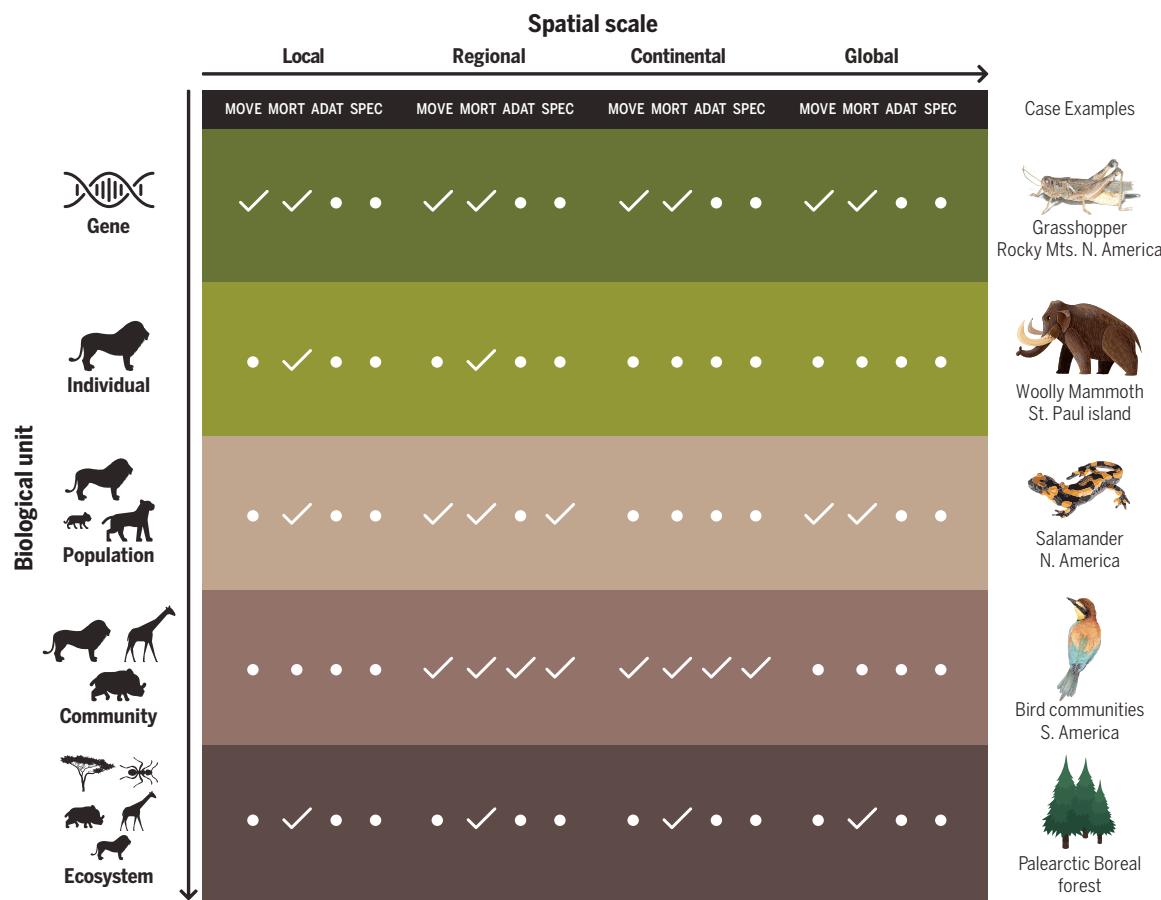
Fig. 5. Simulating mechanisms of past climate-biodiversity dynamics.
Process-explicit models built across different levels of biological organization (gene, individual, population, community, and ecosystem) and spatial scales (local, regional, continental, and global). Ticks indicate ecological and evolutionary processes that have been modeled at these different biological and spatial scales: MOVE, movement; MORT, mortality; ADAT adaptation; and SPEC, speciation. Dots indicate an absence of information. Illustrations show exemplar case studies for different biological organizations: grasshopper (*Melanoplus oregonensis*), Rocky Mountains of North America; woolly mammoth (*Mammuthus primigenius*), St. Paul Island; a salamander (*Plethodontid sp.*), North America; bird communities in South America; and boreal forests in the Palearctic. Details of studies are provided in (*100*). [Image credits: Samuel Barrena, tbob, shaineast, HN Works, flaticon]

Driver-state relationships that can now be simulated include effects of climatic change on migration, adaptation, extinction, and speciation (Fig. 5). However, the number and combination of processes simulated depends on the spatial scale and unit of biological organization being modeled (Fig. 5). Such simulations—which unpack complex patterns of biodiversity, driven by multiple biological processes and agents—enable biotic responses to environmental change to be better contextualized and integrated into future biodiversity management (*13*).

Process-based models also permit in silico experiments on the biological consequences of rates of past climatic and environmental changes, allowing counterfactual hypotheses of eco-evolutionary dynamics to be tested (*82*). Model parameters can be held constant to understand the isolated or interacting effects of other dynamical processes on emergent patterns (*81*). Detailed scenario comparisons have been used to investigate competing explanations for eco-logical regime shifts in the Holocene (*83*), migration patterns of anatomically modern humans since the LIG (*84*), and extirpation patterns during the Pleistocene-Holocene transition (*85*).

Pattern-oriented modeling (POM) of complex paleoecological systems is emerging as a powerful tool (*82*). Spatiotemporal patterns inferred from the paleo-record are used as filters for evaluating whether a model is adequate in its structure and parameterization to simulate the underlying mechanisms. A requirement of POM is that its state variables are expressed in equivalent units to target variables inferred (or measured directly) from paleo-archives. Using paleo-enabled EBVs as targets in POM analysis improves the realism of selected models (those with sufficient structural complexity and adequate parameterization) for conservation management and forecasting.

Looking ahead

Climatologists are taking full advantage of the long-term history of the planet as recorded in paleo-archives to understand mechanisms of long-term climate forcing, quantify trends, and develop scenarios of future climate change (*86*). A wider usage of paleo-archives for quantifying and reporting climate-biodiversity dynamics, particularly in regions where past and future climate change is likely to be similar (Fig. 3), requires an expansion of the taxonomic, spatial, and temporal extent of current paleo-archives. Community-scale genome sequencing of biological remains that are preserved in the permafrost, ice-cores, marine and lake deposits, and coprolites provides solutions for increasing the taxonomic coverage of paleo-samples, often improving knowledge of the geographical distribution of species and ecological communities (*87*). These inferences will be strengthened through robust knowledge of post mortem processes of fossilization (*25*). An expansion of paleo-ecological information in open-access global databases (*88*), including geo-referenced species- and community-level ancient DNA data, will further increase the geographical representation

and temporal coverage of paleo-enabled conservation metrics.

Methods for extending the temporal coverage of past climate-biodiversity dynamics beyond the ~50,000-year age-limit of radiocarbon dating include uranium-thorium dating, optically stimulated luminescence, paleo-magnetism, and infrared stimulated luminescence. However, dates for climatic and biotic events derived from these approaches are generally not resolved at human-relevant time scales (owing to dating limitations and uncertainty), limiting the assignment of ecological shifts to rapid climatic changes during periods earlier than ~30,000 years ago. Tephra layers from volcanic activity, preserved in ice and sediment, have the potential to align paleoenvironmental proxies in space and time for the LD and earlier, making them particularly useful for interpreting biodiversity and ecosystem responses to regional climatic change ([89]).

Individual paleoclimate proxies only approximate broader-scale changes in climatic conditions ([42]); hence, a more thorough understanding of the paleoecology of species and their ecosystems will result from higher spatiotemporal-resolution paleoclimate projections from earth-systems models that use continuous simulations of the transient climate from the LIG to present ([90]). Including improved reconstructions of solar variability, volcanic eruptions, and land-use during the Holocene in these transient simulations will provide a more complete picture of temporal change in regional climates over this period.

Although modern DNA sequencing technologies can generate genetic-based estimates of population change (such as through nuclear single-nucleotide polymorphisms and mitochondrial markers) and adaptive potential to climate change (allelic diversity) ([91]), they have been primarily applied to contemporary or 20th-century samples ([92]). Genomic information extracted from well-preserved fossils is now permitting changes in genetic diversity to be estimated across extended time periods (back at least to the LD) ([93]), informing research on climate change susceptibility and providing preindustrial baseline genomic information for conservation programs, including genetic rescue. Aligning population-level genomic information on inbreeding and connectivity from ancient samples ([94]) with paleoenvironmental proxies presents opportunities to infer magnitudes and rates of change in genetic-based conservation metrics under climate change. Advances that allow changes in allelic diversity to be uncovered from ancient genomes could provide an additional class of paleo-enabled EBV ("genetic composition") relevant to assessing climate-sensitivity and threat status of different taxa.

Decreasing costs of recovering genomic-scale endogenous DNA from fossils are facilitating the compilation of more robust and taxonomically diverse data sets ([95]). This will likely improve understanding of how gene function and gene expression regulate the abilities and speeds at which in situ populations evolve under different rates and magnitudes of climate change, making the inclusion of genomic adaptation in conservation schemes and metrics more feasible ([91]). Indirect paleogenomic evidence suggests a strong potential for fast genomic adaptation to rapid climate change ([96]). However, the generality of these findings (and their potential relevance to rapid warming events) is unknown, given that they are based on a single taxon and small sample sizes.

Simulation and advanced empirical approaches that compare mechanisms of change in nearby regions with different histories of human colonization and land use are likely to further improve knowledge of the synergistic roles of humans and climate in the distributions of taxonomically diverse organisms and communities in space and time. Human-induced landscape transformation on the hundreds of islands in East Polynesia, and potentially Madagascar, did not occur with any severity until within the past millennium ([97], [98]). Detailed comparisons of long-term biodiversity and ecosystem change on these islands, in comparison and contrast with those on islands of comparable size that have longer human histories (such as Fiji, Cuba, and Tasmania), could prove enlightening.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/369/6507/eabc5654/suppl/DC1
Appendix S1: Enhanced Figure Legends
Full Image Sources and Credits
References (*101–110*)

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Using paleo-archives to safeguard biodiversity under climate change

Damien A. Fordham, Stephen T. Jackson, Stuart C. Brown, Brian Huntley, Barry W. Brook, Dorthe Dahl-Jensen, M. Thomas P. Gilbert, Bette L. Otto-Bliesner, Anders Svensson, Spyros Theodoridis, Janet M. Wilmshurst, Jessie C. Buettel, Elisabetta Canteri, Matthew McDowell, Ludovic Orlando, July A. Pilowsky, Carsten Rahbek, and David Nogues-Bravo

Using the past to inform the future

The late Quaternary paleorecord, within the past #130,000 years, can help to inform present-day management of the Earth's ecosystems and biota under climate change. Fordham *et al.* review when and where rapid climate transitions can be found in the paleoclimate record. They show how such events in Earth's history can shape our understanding of the consequences of future global warming, including rates of biodiversity loss, changes in ecosystem structure and function, and degradation in the goods and services that these ecosystems provide to humanity. They also highlight how recent developments at the intersection of paleoecology, paleoclimatology, and macroecology can provide opportunities to anticipate and manage the responses of species and ecosystems to changing climates in the Anthropocene.

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