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 (last ~ 130,000 years). While 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 to 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, test efficacy of threatened-species assessments and resilience of biota during periods of abrupt warming, and locate biogeographic areas that remain stable under shifting climates. Refinement of essential biodiversity variables using past biodiversity dynamics will improve 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 non-climate 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.

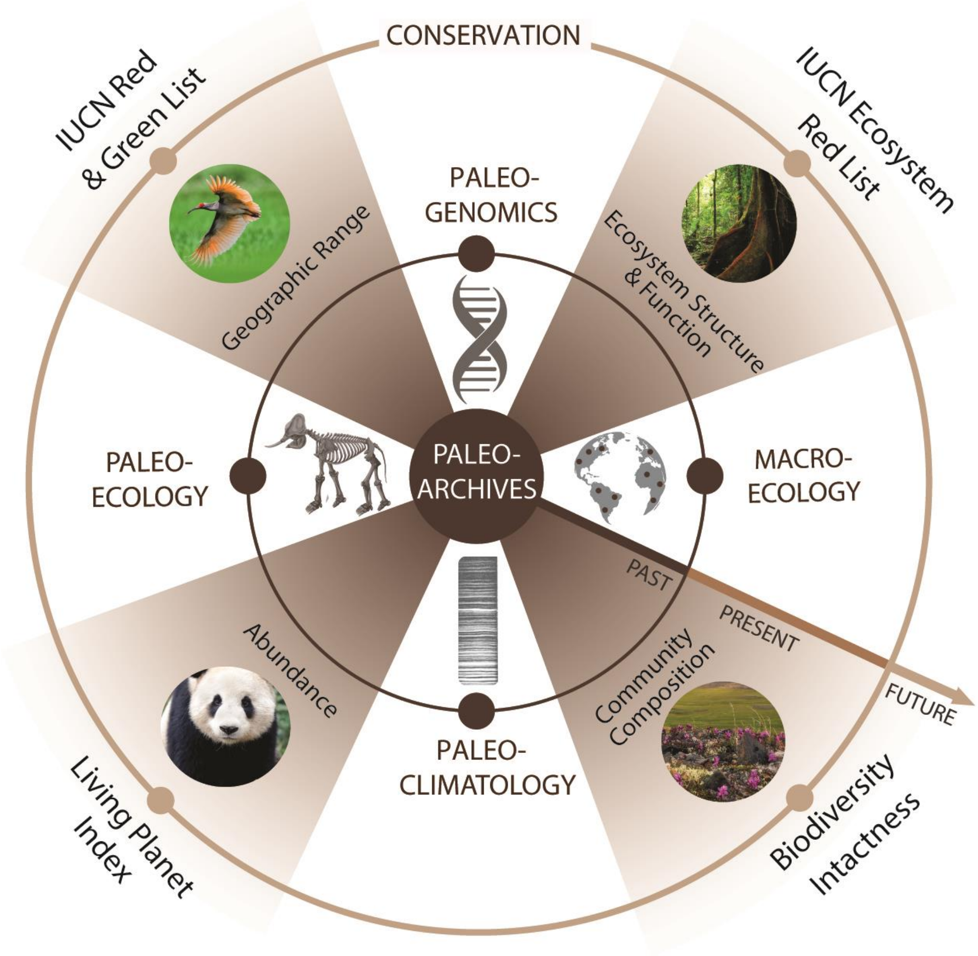

Figure caption: **Paleo-archives offer new prospects for benchmarking and maintaining future biodiversity.** Integrated research using paleo-archives provides empirical foundations for contextualizing climate-driven changes in species populations, community composition, and ecosystem structure and function.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

Title: Using paleo-archives to safeguard biodiversity under climate change

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One sentence summary: Interdisciplinary use of paleo-archives can assist in mitigating climate-driven biodiversity losses and ecosystem change.

Abstract

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 that these advances will bring, 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.

Introduction

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 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 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 at least 20 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 to 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*). Indeed, 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, 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 timescales 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 (based on *16*). Thus, there is enormous potential to use geohistorical data to better derive and strengthen 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, due to 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 by deliberate experiments or direct monitoring.

Late Quaternary intervals comparable to near-future climate projections include the Holocene Thermal Maximum (HTM) between 12 and 5 k BP (thousands of years before the present) (*28*, *29*), in which regional surface temperature anomalies relative to pre-industrial climates were + 3° C or more (Fig. 1), and the earliest millennia of the last interglacial (LIG, 129 to 111 k BP), when the global mean temperature anomaly was > 1 °C above pre-industrial conditions (*10*). Summer warming was prominent in Northern Hemisphere continental interiors during these periods; in contrast, ocean warming was comparatively small (Fig. 1). Deeper-time warm intervals include the Early Eocene (ca. 50 Ma) and the Mid-Pliocene (3.3-3.0 Ma), when atmospheric CO_2 concentrations were greater or comparable to present; mean annual surface temperatures were >10 °C (Early Eocene) and ~ 3 °C warmer (Mid-Pliocene) than pre-industrial 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 northwards in Central Siberia (*30*), while the prairie–forest boundary on the North American Great Plains shifted ~ 200 – 250 km eastward under increased aridity (*31*). Montane tree-lines were lower than today in the Southern Ocean region during HTM, owing to drier conditions under higher temperatures (*29*). In much of northern sub-tropical Africa, HTM climate was wetter (though cooler) than today, due largely to higher summer temperatures in the northern Sahara (Fig. 1) leading monsoon rains to extend further north, allowing many savanna plants (and riparian and wetland animals) to extend their ranges northwards by ~ 400–500 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 1,000 m downslope (*33*).

During the LIG, boreal forests extended north into Greenland (*34*), while 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 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 underscores 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 and 18 k BP, 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 to 10 k BP), many terrestrial regions experienced temperature increases of 4 to > 10 °C (Fig. 2). Some were gradual, but others occurred during episodes spanning 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 14.7 and 11.7 k BP, 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 3-5 °C during the 14.7 k BP event (*45*). While 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 k BP suggest that 39 % of terrestrial Earth experienced near-centennial climate shifts of similar magnitude to 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 paleoecological records, providing natural laboratories for better anticipating biotic responses to climatic changes.

Past rapid warmings profoundly impacted 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 5- to 15-fold population-size reductions, 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 14.7 k BP warming event in temporary cool refugia (*48*), while 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 below-ground 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 (e.g., decreasing albedo, 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 (Fig. 2 & 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 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 non-stationary Holocene climate variability and its interactions with long-distance dispersal, local demographic processes, and species life-history traits (*56-59*). Moreover, Holocene records show 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*), while its geographic distribution held steady during a dramatic range-wide population decline (*61*). The latter example represents a rapid ecosystem transformation, whereby 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 underlying 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 underway 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 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, since EBVs comprise 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), using count data, or from genes in extant populations, using coalescent estimates of effective population size (see examples 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 to the abundance-based indicators of biodiversity change used today in conservation policy [Living Planet Index, IUCN Red List and IUCN Green List] and assessment of biodiversity targets [Convention on Biological Diversity (CBD)] in the face of anthropogenic climate and environmental change (*69*).

Since warning signals of biotic transitions or state-shifts are commonly identified 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 significant 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 climate had in past range contractions and expansions (see Fig. 4, Muskox; *Ovibos moschatus*). Furthermore, paleo-enabled conservation variables allow morphological changes within species populations to be measured across time (*22*) (Fig. 4), providing a deeper understanding of species-level responses to climate change (*73*) and improved 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 *(72; Fig. 4)*. This can directly affect evaluations of conservation status (IUCN Red List) and measures of conservation success (IUCN Green List) (*75*). While 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 strategies. However, if applied indiscriminately, this could result in extinctions of species whose persistence may depend upon populations close to the periphery of their historical ranges (according to paleo-archives) (*76*). Inferences of range shifts during the late Quaternary offer unique 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 resilience of ecosystem services to climate variation and change (*78*). Community reconstructions of taxonomic richness 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 following 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 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 unique 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. 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 ecological 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-orientated modeling (POM) of complex paleoecological systems is emerging as a powerful tool (*82*). Spatio-temporal 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 (i.e., 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 preserved in the permafrost, ice-cores, marine and lake deposits, and coprolites provide 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 paleoecological 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 ka 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 not, generally, 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 ka. 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, using 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.

While modern DNA sequencing technologies can generate genetic-based estimates of population change (e.g., via 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 thereby providing pre-industrial baseline genomic information for conservation programs, including genetic rescue. Aligning population-level genomic information on inbreeding and connectivity (F_{st}) from ancient samples (*94*) with paleo-environmental 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 is 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 on 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 last 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 (e.g., Fiji, Cuba, and Tasmania) could prove enlightening.

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Supplementary Materials:

Appendix 1: Enhanced figure legends
References (101-110)

Fig. 1. Similarity in temperatures between past warm periods and the near future. Boreal summer (JJA) land and sea-surface projected temperature changes from a pre-industrial baseline for the last interglacial (~127 k BP; **A**), mid-Holocene (~6 k BP; **B**), and 2030 under RCP 4.5 (**C**). Black areas in **A** and **B** represent locations with temperature anomalies that are congruent with **C.** Boxes **1-4** show biotic responses inferred from paleo-archives (insets), with arrows pointing to the relevant time periods. Paleo-archives include fossil bones (1 & 2) and pollen in sediment cores (3 & 4). Triangles in 1 show fossil sites. Paleoclimate simulations are detailed in Appendix 1.

Fig. 2. Abrupt warming during the last deglaciation. Temperature change (°C; y-axis in panels **A**-**E**) since 20 k BP (x-axis) or the earliest record after 20 ka (A5, C 6, D 9, E12) for 12 paleoclimate reconstructions (*29, 99*) from 8 zoogeographic realms (*46*), including Antarctica (**A-E**). Boxplots (**F**) show a multi-model averaged forecast of annual-mean temperature change for 2080 from a baseline focused on 1990 (*16*) under two radiative-forcing scenarios. Note that the y-axis scale differs in A-F. Details of paleoclimate reconstructions in **A**-**E** are provided in Appendix 1.

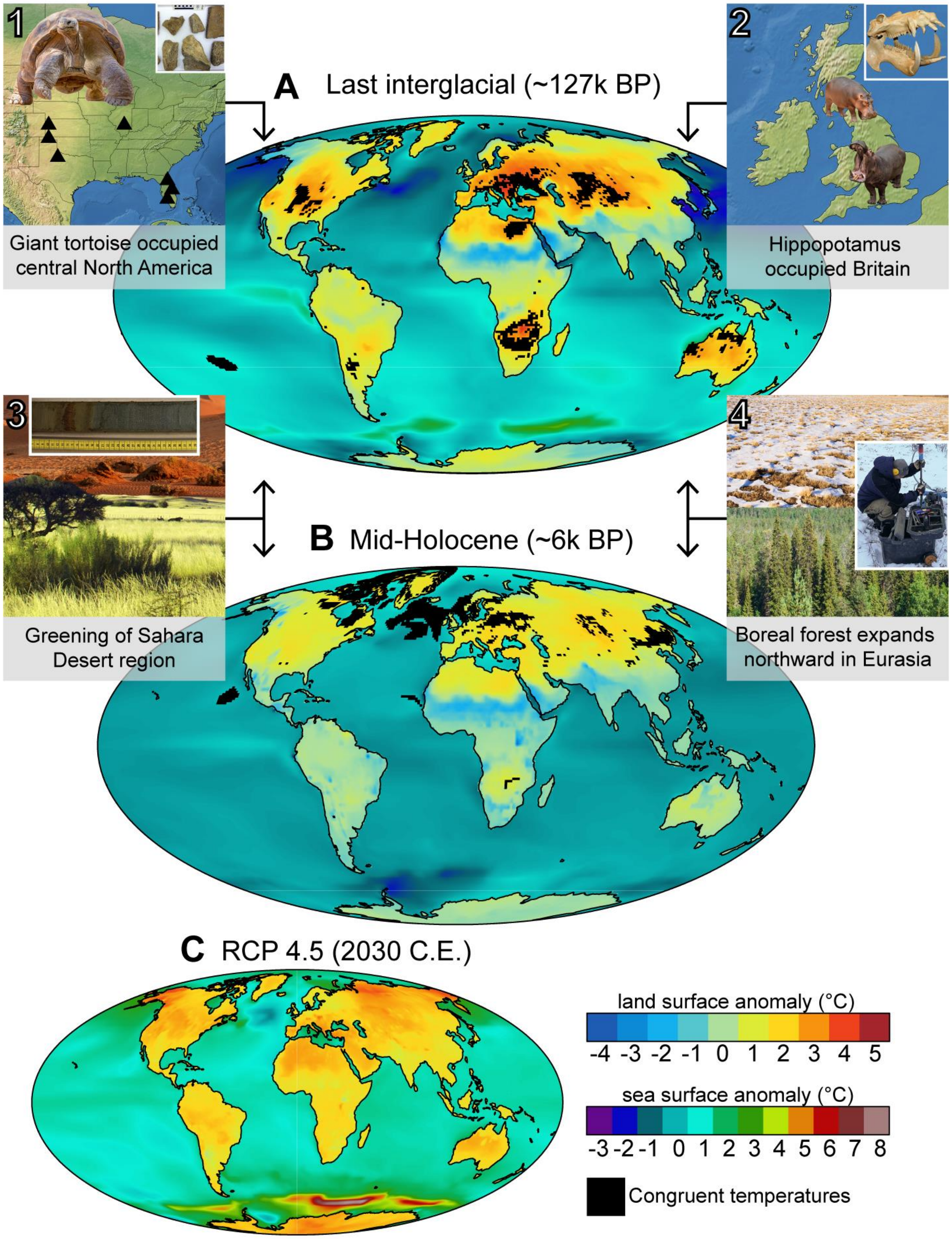
Fig. 3. Similarity in past and future rapid temperature shifts. Map shows overlap (%) in the signal-to-noise ratio (SNR) of rapid climate change events for past (21 k BP to 1850 CE) and future (21st century, RCP 8.5) temperature change in zoogeographic regions (*46*). Colors represent the % overlap in SNR. Plots (**A**-**D**) show SNR distributional overlap (green = past and red = future) within the Arctico-Siberian (**A**; 64 %), Eurasian (**B**; 72 %), Amazonian (**C**; 55%), and Novozelandic (**D**; 52%) regions. Pictures show examples of ecosystems in regions (**A**-**D**)

with geohistories suitable for assessing and maintaining future biodiversity. Data is based on (*16*). Distributional overlaps for all zoogeographic regions are provided here (*100*).

Fig. 4. Paleo-archives for informing conservation under climate change. Paleo-archives (DNA, fossils, sediments, including in silico computational reconstructions) provide "log books" of changes in species distributions (**A**) and abundances (**B**-**D**), traits (**E**), community compositions (**F**), and ecosystem structures and functions (**G**-**H**). Projected (**A**) geographic range (km^2*10^6) and (**B**) effective population size (Ne *1000) of muskox (*Ovibos moschatus*); (**C**) Mammal relative abundance, southern Australia (*Pseudomys australis* [red], *Rattus fuscipes* [orange], *Pseudomys apodemoides* [yellow]); (**D**) Plant relative abundance, southern Italy (*Albies alba* [red], *Fagus sylvatica* [orange], *Carpinus betulus* [yellow]); (**E**) Woodrat (*Neotoma cinerea*) body mass, Great Basin USA; (**F**) Taxonomic richness of plants in southern Italy (dark blue) and Guatemala (light blue); (**G**) Net primary productivity, North America (grey), and plant biomass (black), eastern Canada; (**H**) Projected area (km^2*10^6) of savanna ecosystem, India. Relevant conservation schemes: 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). X-axis shows time BP in thousands (k) of years. Trajectories shown **A**-**H** are detailed in Appendix 1.

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 show ecological and evolutionary processes that have been modeled at these different biological and spatial scales: MOVE (movement), MORT (mortality), ADAP (adaptation), and SPEC (speciation). Dots show 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 here: (*100*)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Giant tortoise occupied central North America
2
Hippopotamus occupied Britain
A Last interglacial (~127k BP)
3
Greening of Sahara Desert region
4
Boreal forest expands northward in Eurasia
B Mid-Holocene (~6k BP)
C RCP 4.5 (2030 C.E.)
land surface anomaly (°C)
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sea surface anomaly (°C)
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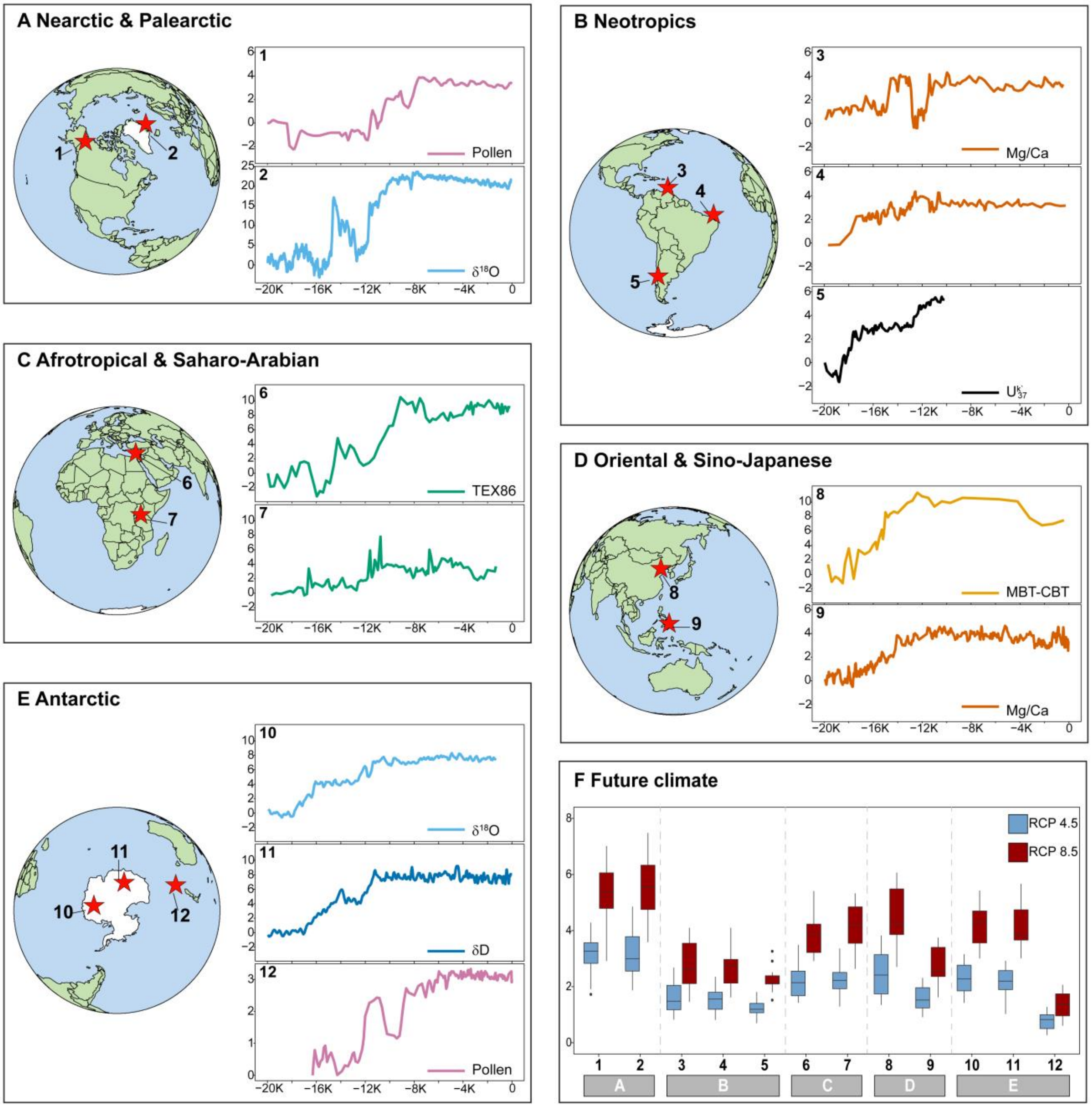
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D Oriental & Sino-Japanese
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MBT-CBT
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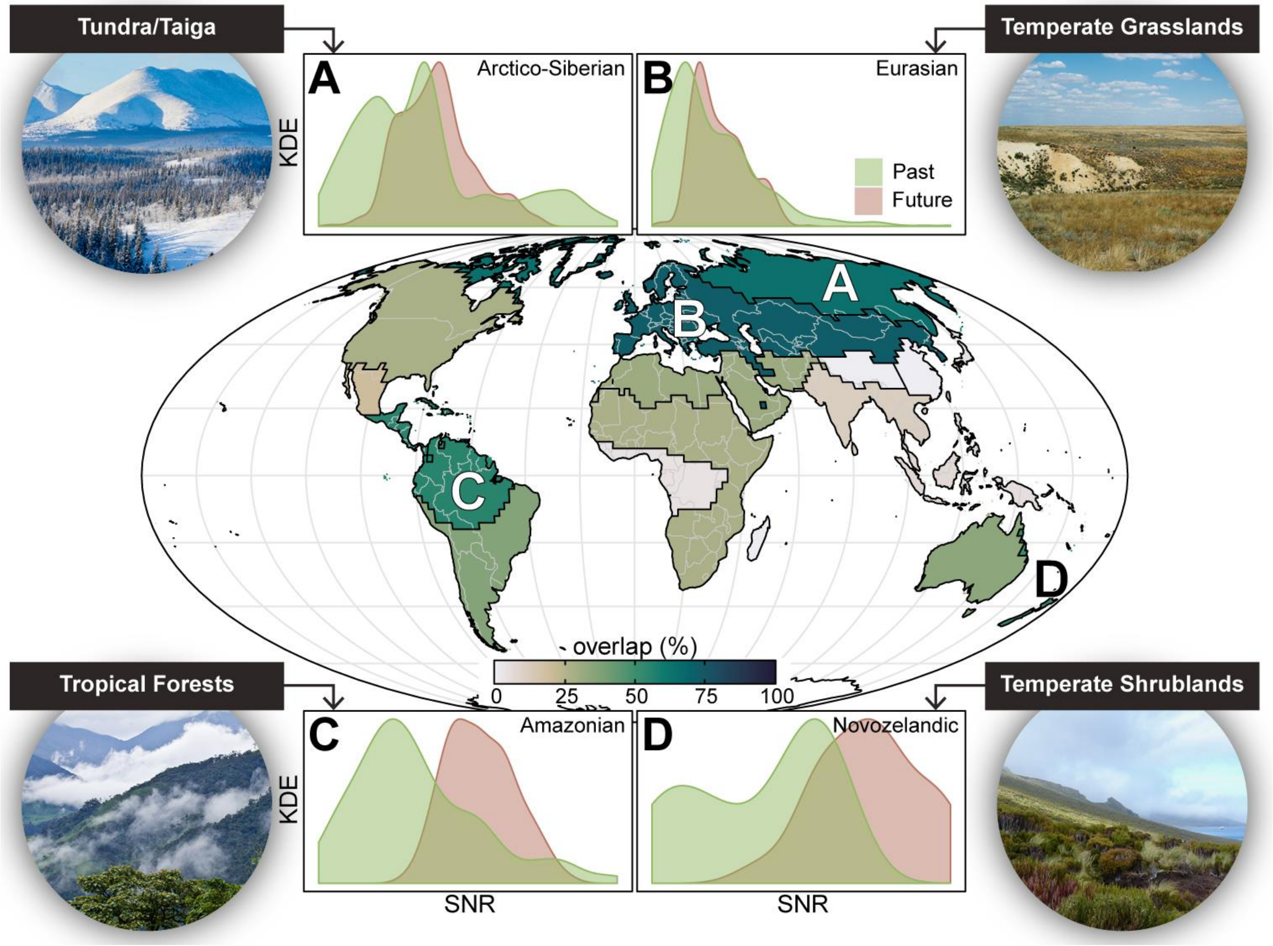
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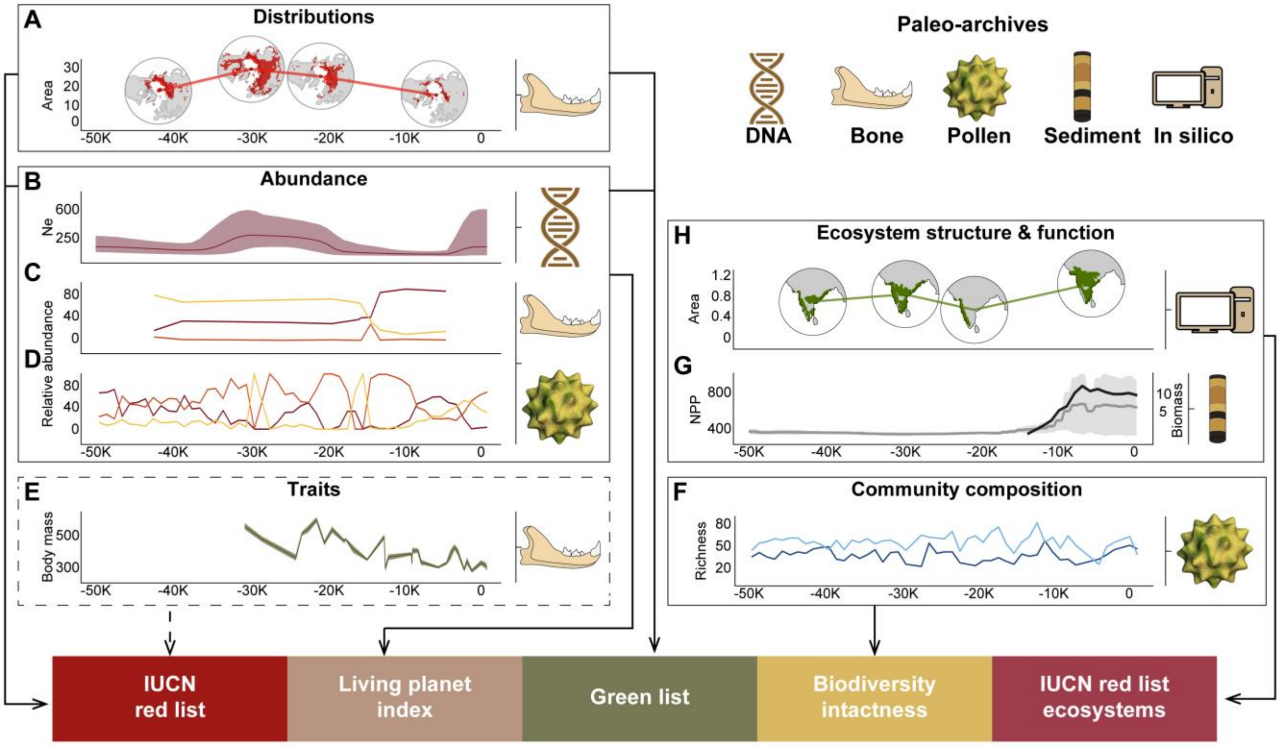
Temperate Shrublands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B
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250
C
80
40
0
D
Relative abundance
80
40
0
-50K
-40K
-30K
-20K
-10K
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E
Traits
Body mass
500
300
-50K
-40K
-30K
-20K
-10K
0
Paleo-archives
DNA
Bone
Pollen
Sediment
In silico
H
Ecosystem structure & function
Area
1.2
0.8
0.4
0
G
NPP
800
400
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Biomass
-50K
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Community composition
Richness
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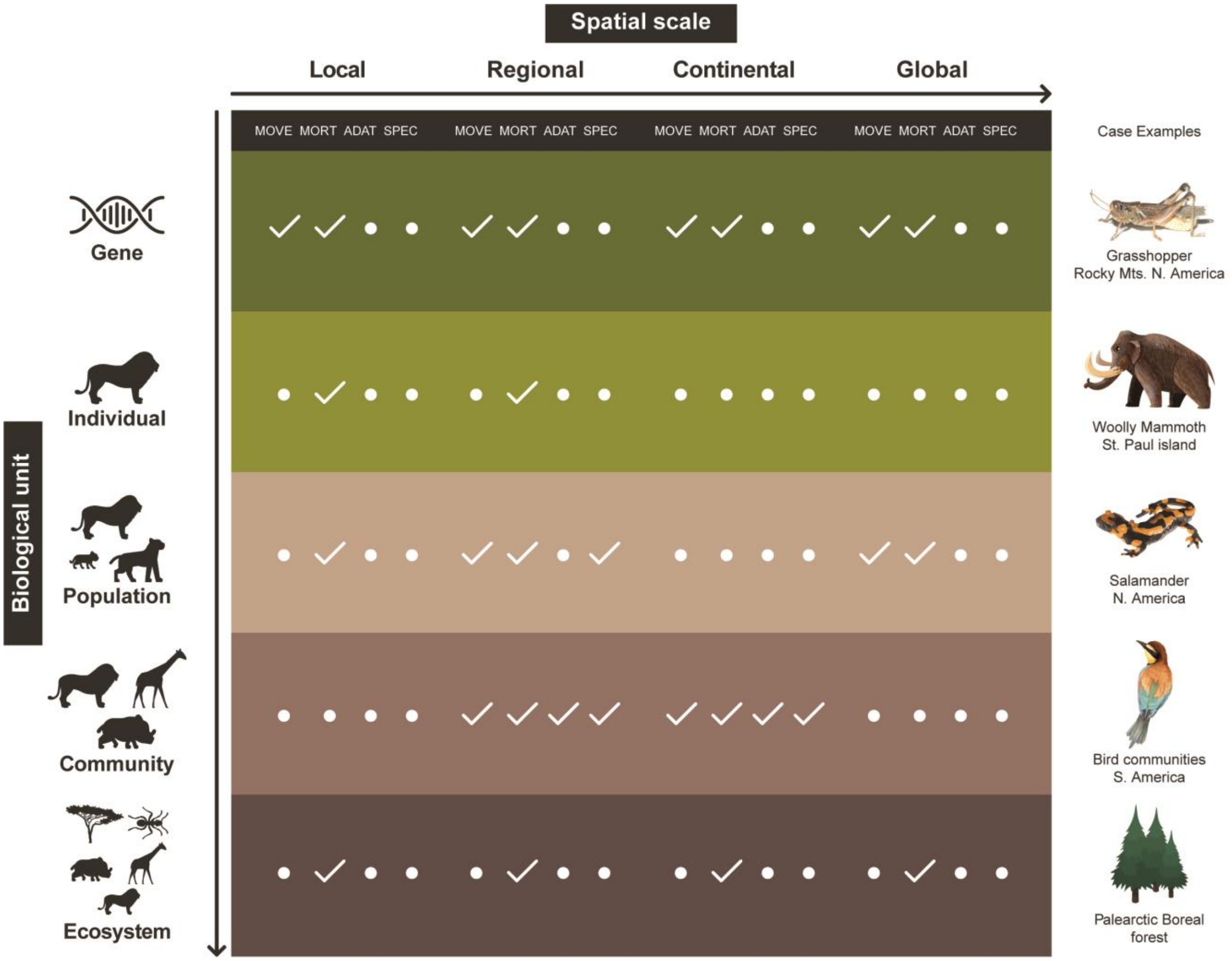

	Local				Regional				Continental				Global				
	MOVE	MORT	ADAT	SPEC	MOVE	MORT	ADAT	SPEC	MOVE	MORT	ADAT	SPEC	MOVE	MORT	ADAT	SPEC	Case Examples
Gene	✓	✓	●	●	✓	✓	●	●	✓	✓	●	●	✓	✓	●	●	Grasshopper Rocky Mts. N. America
Individual	●	✓	●	●	●	✓	●	●	●	●	●	●	●	●	●	●	Woolly Mammoth St. Paul island
Population	●	✓	●	●	✓	✓	●	✓	●	●	●	●	✓	✓	●	●	Salamander N. America
Community	●	●	●	●	✓	✓	✓	✓	✓	✓	✓	✓	●	●	●	●	Bird communities S. America
Ecosystem	●	✓	●	●	●	✓	●	●	●	✓	●	●	●	✓	●	●	Palearctic Boreal forest

Supplementary Materials for

Using paleo-archives to safeguard biodiversity under climate change

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Appendix 1 Enhanced Figure Legends
References (101 -110)

Enhanced Figure Legends

Fig. 1. Similarity in temperatures between past warm periods and the near future. Boreal summer (June, July, August) temperature anomalies from pre-industrial conditions for the earlier millennia of the last inter-glacial (~127 k BP; **A**), midway through the Holocene (~6 k BP; **B**), and early in the 21st Century (2030 CE; **C**) are based on the Community Climate System Model 4 (CCSM4) (*101*). The 127 k simulation used the CMIP6/PMIP4 protocols as described in Otto-Bliesner et al., (*90*). The 6 k BP and future projection were taken from the Coupled Model Intercomparison Project 5 (CMIP5; *102*) and were extracted through the Earth Science Grid Federation (https://esgf-node.llnl.gov/projects/esgf-llnl/). The 2030 projections are under a Representative Concentration Pathway (RCP) 4.5 scenario (*103*). Pre-industrial conditions are based on multi-century unforced CCSM4 climate simulations (e.g. non-evolving land use and greenhouse gas concentrations), where the initial conditions are set based on atmospheric gas concentrations prior to large-scale industrialization (*101*, *102*). For CCSM4 the pre-industrial control runs have the following constant forcing – incoming solar radiation at the top of atmosphere is 1360.9 W/m^2, and the CO_2 level is set to 284.7 ppm, while other aerosol concentrations are specified from a historical run (*101*). Pre-industrial conditions are, therefore, the average temperature data for Boreal summer months (JJA) across all years of a multi-century unforced climate simulation (n = 1,051 years) (*16*). Areas of congruence between projected anomalies for 127 k BP and 2030 CE and between anomalies for 6 k BP and 2030 CE (Fig. 1) are mapped using anomalies binned to the nearest 1°C.

Fig. 2. Abrupt warming during the last deglaciation. Temperature reconstructions are from high-resolution paleoclimate proxies (*29*, *99*). Eleven paleoclimate records (Fig. 2 inset graphs 1-11) are from Shakun et al. (*99*) and one (Fig. 2 inset graph 12) is from McGlone et al. (*29*). Metadata for the selected cores is shown in (*100*). Due to large variation in the temporal resolution of the paleoclimate proxies (mean = 141, S.D. = 112, range = 377 years), records with temporal resolutions finer than the mean (Fig. 2 inset graphs 1-5, 9-12) were smoothed so that their temporal resolutions were equal to the mean value. All temperature records have been converted to anomalies (°C) from either 20 k BP for records that extended beyond 20 k BP, or from the earliest time step for those that did not extend past 20 k BP (Fig. 2 inset graphs 5, 6, 9, 12). Future temperature anomalies at each site with a paleoclimate reconstruction (**F**) show the projected multi-model average difference between the 30-year annual temperature centered on 1990, and that centered on 2080 under both RCP 4.5 and RCP 8.5 scenarios (*103*) for 18 different CMIP5 AOGCMs (*16*). RCP 4.5 is an intermediate warming scenario with radiative forcing levels reaching approximately 4.5 W/m^2 by 2100, while RCP 8.5 is a high warming scenario with radiative forcing levels reaching approximately 8.5 W/m^2 by 2100 (*103*). Boxplots show the median and range in future estimates of temperature conditions for each site. Model projections were bilinearly interpolated to 2.5° x 2.5° (longitude x latitude) from the nominal resolutions for each of the models to make sure all models were on a common grid before calculating multi-model averages (*16*).

Fig. 4. Paleo-archives for informing conservation under climate change (**A**) Changes in the area (km^2 *10^6) of the geographical range of muskox (*Ovibos moschatus*) inferred from georeferenced and dated fossil records, paleoclimatic simulations, and species distribution models at four different periods (42, 30, 21, and 6 ka) based on Lorenzen et al. (*47*). (**B**) Plots of effective population size (N_e*1000) of the muskox for the last 50,000 years based on ancient DNA (aDNA) from 138 GenBank records and coalescence modelling (*100*). (**C**) Change in relative abundance (%) for three rodent taxa (*Pseudomys australis*, *Rattus fuscipes*, *Pseudomys apodemoides*) from Naracoorte cave (Australia) at 42.9, 39.3, 26.2, 20.1, 16.7, 16.3, 15.1, 13.9, 10.6, and 5.4 k BP (*104*, *105*). (**D**) Change in relative abundance (%) for three plant taxa (*Carpinus betulus*, *Abies alba*, *Fagus sylvatica*) at Monticchio lake (Southern Italy) at millennial timesteps (0 – 50 k BP) (*100*). (**E**) Woodrat (*Neotoma cinerea*) body mass (g) estimates over the last thirty thousand years using 94 paleo-middens from Titus Canyon, Death Valley (US) (*106*). (**F**) Plant taxonomic richness at the genus level for Monticchio lake (*107*) and at Peten Itza lake (Guatemala) (*108*) based on relative abundances and raw pollen counts, respectively. Methods used to transform relative abundance data into presence/absence type are described here (*100*). (**G**) Above ground tree biomass (grey line; petagrams) for six tree genera (*Abies*, *Acer*, *Betula*, *Picea*, *Pinus*, and *Populus)* for one-thousand year time intervals (14 ka to 0 ka) across eastern Canada (*109*). Simulated changes in net primary productivity (NPP*0.1; gC/m^2/yr) for the North American zoogeographic region (*46*) over the last fifty thousand years (50 k BP – 0 k BP) at a spatial resolution of 1 x 1 ° and a temporal resolution of 25 years (*110*). Plots show mean (black line) and ± 1 standard deviation calculated for each time interval (light grey shading). (**H**) Changes in area (km^2 *10^6) of savanna in Asia for four time periods (42, 30, 21, and 6 k BP)

based on coupling the HadCM3 coupled atmosphere–ocean general circulation model with the LPJ-GUESS dynamic global vegetation model (DGVM) (*100*).

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