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Halting climate-driven biodiversity change with paleo-archives

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Enhanced abstract [600 words max]

Background: The effects of global climate change on biodiversity have now been documented across every biome on Earth. Safeguarding biodiversity and the structure and function of ecosystems against future climate changes demands accurate predictions and effective solutions. Research emerging at the frontiers between paleoecology, paleogenomics, paleoclimatology and macroecology offers new prospects for anticipating and managing responses of biodiversity to climate-related environmental change. By unveiling the ecological and evolutionary mechanisms that have shaped past and present-day patterns of biodiversity, this frontline in paleo-research is providing an empirical foundation for better anticipating what the future may bring under accelerated climate change. Advances are being driven by developments in high-throughput sequencing, dating and computational technologies, ecological simulation models, and improvements in the spatiotemporal resolution of paleoenvironmental data, particularly for the late Quaternary (last ~ 130,000 years). While these advances are providing a new understanding of past responses of biodiversity to global change, benefits for improving forecasting of biodiversity impacts from climate change and informing future conservation policies are being missed. We showcase how the late Quaternary paleo-record can be used to derive policy-relevant insights, contributing toward more effective management of the Earth's ecosystems and diverse biota under future climate change.

Advances: The profound threat of climate change demands that conservationists seek ever more effective ways of improving the outlook for biodiversity and ecosystems. Analytical approaches that combine high-resolution paleoclimate proxy and/or simulation data, fossil material with high-precision dates and high-quality ancient DNA provide opportunities to unveil biotic responses to various rates and magnitudes of climate warming, some being comparable to 21st century forecasts. These reference periods in Earth's history provide laboratories for testing fundamental theories in ecology and evolution using macroecological models; and connecting these to the on-ground design and implementation of effective measures to protect biodiversity. Opportunities for conservation include identifying ecological processes that cause species to be differentially prone to regional and range-wide extinction, testing if threatened-species assessments work and locating habitats that support stable ecosystems in the face of shifting climates. Direct application of past biodiversity

dynamics to future management will be made more straightforward through the refined use of “essential biodiversity variables” (EBVs), which can measure the broad footprint of past climate change on biodiversity, providing better knowledge of climate driven shifts in species populations, community composition and ecosystem structure and function. This will allow present-day early warning systems and conservation paradigms to be tested and refined at spatiotemporal scales that are directly relevant to conservation policymakers, providing a more informed understanding of thresholds for species- and ecosystem-level collapse, resulting in better systematic conservation planning.

Outlook: As paleo-archives become more commonly integrated into conservation science, conservation guidelines for the management of biodiversity and ecosystems will benefit from understanding how different spatiotemporal scales of past climate change and perturbations have affected different levels of biological organization across the planet. Achieving this will require global initiatives to harmonise vast numbers of paleoclimate-proxy and paleoecological records, and high-spatiotemporal resolution paleoclimate projections from a wide number of earth-system models. There will also need to be a greater focus on using paleoecological data to disentangle climate and non-climate impacts on biodiversity and ecosystem function using simulation models and analytical techniques, which compare mechanisms of biodiversity and ecosystem change in nearby regions with very different histories of human colonisation and land-use. Moreover, developments in paleogenomics that pinpoint adaptation across species and populations will be useful in unveiling the microevolutionary processes that can enhance the resilience of biodiversity to climate change. Our recommendations for utilising paleo-archives in conservation policies enhance understanding of the threat of climate change to natural systems, providing decision-makers with improved measures to reduce change in biodiversity from climate change in the Anthropocene.

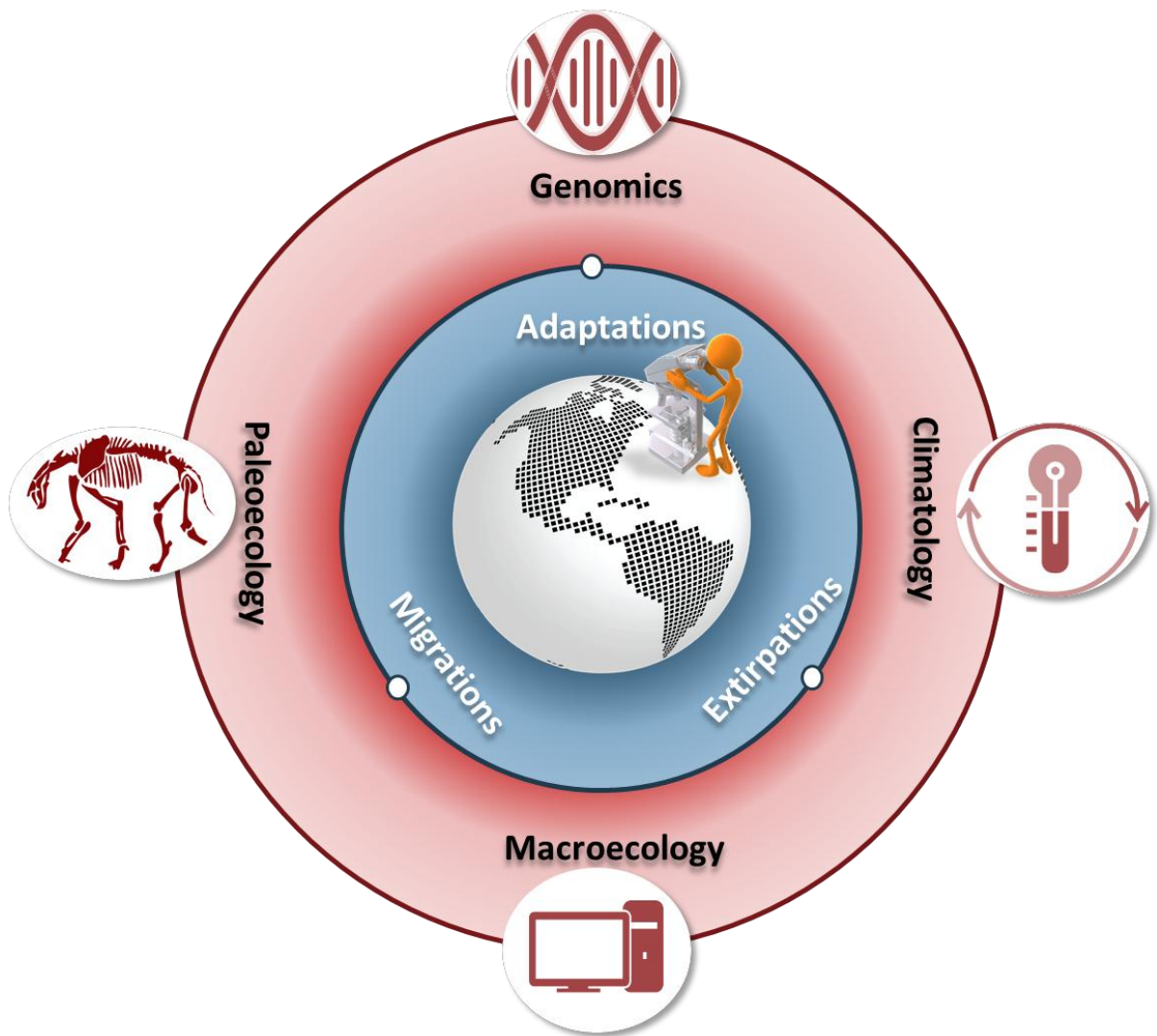


Figure 0: Past natural laboratories will enhance conservation of biodiversity.

Introduction

Global mean temperatures, today, are at the upper edge of interglacial conditions experienced over the past 1.2 million years (1), and their effects are being documented across every biome on Earth (2). As climate disruption intensifies in coming decades, safeguarding biodiversity and the services ecosystems provide to nature and people against further consequences of global warming will remain high on the international policy agenda (1-5). Successful intervention will require conservation actions based on accurate predictions and effective solutions (3). However, robust forecasts of species- to ecosystem-level responses to changing climates have proven difficult to formulate (4), adversely affecting conservation planning (5).

Research at the intersection of paleoecology, paleoclimatology, paleogenomics and macroecology is offering new prospects for better anticipating and managing responses of biodiversity and ecosystems to climate and associated environmental change. By revealing ecological and evolutionary mechanisms that have shaped past and current-day patterns of biodiversity, this research is providing (i) an empirical foundation for better projecting the broad footprint of accelerated rates of climate change on natural systems; and (ii) greater focus on long-term processes that govern climate-biodiversity dynamics in conservation plans for species and ecosystems (6-8). These new cross-disciplinary approaches for uncovering past responses of diversity to global environmental change are the result of methodological developments in high-throughput sequencing, better dating and computational technologies, advances in ecological and evolutionary simulation models, improvements in the spatiotemporal resolution of paleoclimate simulations, and open access to curated georeferenced and dated fossils, collections of genetic sequences.

Although human land-use and exploitation remain the primary drivers of recent losses of biodiversity (9), climate change is projected to become equally or more important in coming decades (10). This profound threat of future climate change on natural systems demands that conservation biologists and practitioners seek ever more effective ways of improving the outlook for biodiversity and ecosystem structure and function (3, 4). Paleo-archives allow biodiversity responses to climate perturbations to be followed *in situ* as time-series spanning centuries to multiple-millennia. Consequently, past warming intervals provide critical reference points in Earth's history that can be used as natural laboratories to identify biota most vulnerable to rapid climate change (6, 8), and connect theory to the on-ground design and implementation of effective measures to protect biodiversity (7). This is

because the majority of species on Earth today have existed for hundreds of thousands to millions of years (11), and at these timescales there have been at least 20 glacial/interglacial cycles, glacial periods being punctuated and terminated by rapid regional warming events, occurring over periods as short as decades (12). In many zoogeographic regions, these events are comparable in pace and magnitude to 21st century forecasts (13).

Although past warming events are not direct analogues of future global warming, because of different regional patterning of these climate events and much colder initial baselines (14), they provide potentially important windows for examining species- and ecosystem-level responses to abrupt changes in climate. In fact, one of the most powerful features of the paleo record is its heuristic nature, providing opportunities to generate “thinking tools” that can be used to anticipate and visualise ecological consequences of future climate change based on realised past events.

Access to a combination of fossil material with more precise radiocarbon dates, high-quality ancient DNA and climate simulations with sufficient temporal resolution for reconstructing abrupt climate change events, has meant that the late Quaternary (last ~ 130,000 years) is providing new and effective opportunities to understand better the effects of climate change on the dynamics of biodiversity and the structure and function of ecosystems, potentially strengthening conservation outcomes in the face of future climate change (8, 15). For example, by connecting ecological and evolutionary models with inferences of past responses of biodiversity to climate change, there is capacity to formulate a better understanding of why species’ population sizes and distributions change over time, and why some species survived pronounced climatic shifts and others did not (16). This includes a stronger knowledge of the mechanisms by which species have coped with high rates and magnitudes of climate change at spatiotemporal scales that are directly relevant to common vulnerability assessments, based on sensitivities and adaptive capacities to climate change (5).

With a growing emphasis on integrating paleobiology into conservation biology (17-20), clear guidelines are needed that define when, where and how scientists can use the late Quaternary paleo-record to provide important insights for conservation policy-makers, enabling them better to direct the responsible management of the Earth’s ecosystems and diverse biota under trajectories of future climate change. Here we pinpoint where and when climate transitions on human-relevant timescales can be found in the paleoclimate record and

show how these reference points in Earth's history can be used as natural, unplanned experiments for anticipating and managing the likely consequences of future global warming on rates of terrestrial biodiversity loss and their effects on ecosystem properties, including the goods and services they provide to humanity. We show that ~40 % of terrestrial earth is projected to have experienced past warming events that are similar in pace and magnitude to future forecasts at the scale of zoogeographic regions. These areas provide critical laboratories for studying and halting climate-driven biodiversity change.

Ancient warm periods and biodiversity consequences

Earth has experienced conditions warmer than the 20th Century, globally and locally, during both the Quaternary and the Tertiary (21, 22), providing numerous opportunities to examine what a warmer world looks like ecologically. While these past intervals (like abrupt glacial/interglacial warming events) are not direct analogues for a greenhouse-warming future (23), they 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 experiments.

Late Quaternary intervals comparable to near-future climate projections include the Holocene Thermal Maximum (HTM) between 12 and 5 ka (24, 25), when in some regions surface temperature anomalies relative to pre-industrial climates were 3° C or more (Fig. 1), and the earlier millennia of the last interglacial (LIG, 129 to 116 ka), when the global mean temperature anomaly was 1.3 °C warmer than pre-industrial conditions (22), with more pronounced seasonal increase of land-surface temperature at mid to high latitudes (Fig. 1). Effects were particularly prominent during summer in Northern Hemisphere continental interiors, decreasing in intensity from high to low latitudes (24); effects on sea surface temperatures were small (Fig. 1). More distant warm intervals include the Early Eocene (ca. 50 Ma) and the Mid-Pliocene (3.3-3.0 Ma), under atmospheric CO₂ concentrations greater than or comparable to present; mean annual surface temperatures were >10 °C (Early Eocene) and 3 °C warmer than pre-industrial temperatures (Mid-Pliocene) (21).

During the HTM, warmer temperatures and differing moisture regimes led to climate-driven movements of biome boundaries, and elevational shifts in montane vegetation belts, in many regions. For example, the tundra–forest boundary shifted ~ 200 km northwards in

Central Siberia under warmer temperatures (26), while the prairie–forest boundary on the North American Great Plains shifted ~ 200–250 km eastward in response to increased aridity (27). In the Southern Ocean region, HTM climate was drier and warmer than today, providing unfavourable growing conditions for trees, lowering montane tree-lines (25). In large parts of northern sub-tropical Africa, HTM climatic conditions were wetter (though cooler) than today, due to increased summer temperatures in North Africa (Fig. 1), causing monsoonal rains to penetrate the Sahara Desert, allowing many savanna plant species (and riparian and wetland animals) to extend their ranges northwards by ~ 400–500km (28).

During the LIG, boreal forests extended north into Greenland (29), while the Sahara Desert region was largely occupied by savanna (30). In Europe, warm temperatures allowed Hippopotamus (*Hippopotamus amphibious*) to expand its range as far north as Britain (31). LIG occurrence of giant tortoise *Hesperotestudo* (*Geochelone*) *crassiscutata* in the American Midwest implies temperatures above freezing throughout the year (32); subfreezing temperatures occur in the region today for 5-6 months of the year. Mid-Pliocene warming caused similar latitudinal displacements in vegetation, including poleward contractions of tundra, northward expansions of boreal forest and greening of the Sahara (33). Moreover, during this period of amplified warming and ice sheet retreat, tundra-like communities with dwarf-shrub species of southern beech (*Nothofagus beardmorensis*) were present at high altitudes in Antarctica (34) where today there is polar desert.

By providing estimates of the maximum extents of species' migrations and biome shifts on different continents and in different climatic zones, these past warm periods underscore the need for species to be able shift their range boundaries by $10^2 - 10^3$ km in response to regional warming of magnitudes comparable to those projected for the near future. They also lead to expectations that many species will respond individually to future climatic changes, resulting in communities and ecosystems without modern analogues (35). Importantly, these mechanisms of biodiversity and ecosystem change are unlikely to differ, at least qualitatively, in the future.

Ecological consequences of rapid warming

Between 21,000 and 18,000 years ago, the earth began to emerge from a cold glacial climate, with low CO₂ concentrations and large ice sheets, into the current warm Holocene interglacial (36). During the net global warming of the last deglaciation (LD, 20 to 10 ka), terrestrial

regions experienced temperature changes of as much as 5 to 20 °C (Fig. 2). Some were gradual, but others occurred during rapid-warming episodes spanning decades to centuries. These rapid climate shifts were in some regions up to half as large as the entire difference between glacial and modern conditions (37).

Greenland ice-core records reveal abrupt large-magnitude warming events 14.7 and 11.7 ka, interrupted by at least one transient cooling reversal 12.9 ka, when temperatures in some regions returned to glacial values (12). Warming rates of ~ 10 °C spanning a few years (e.g., the 14.7 event) to a few decades (e.g., 11.7 event) in Greenland (38) are similar to rates forecast for Northern Hemisphere polar regions under greenhouse gas emissions intensive scenarios (Fig. 2). In Europe, rapid warming at onset of the 14.7 event caused increases of 3-5 °C (39) in less than a century (40). While regional climates over the North Atlantic region and Europe reorganised quickly during the LD warmings, signatures of these abrupt events are found globally at varying amplitudes, 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 (37). Paleoclimate simulations show that 39 % of terrestrial earth experienced near-century LD warming events of similar magnitude to future forecasts at the scale of zoogeographic regions under greenhouse gas emission intensive scenario (13; *Supplementary material*). Regions with the largest overlap between past and future warming, include Arctic-Siberia, Eurasia, Amazonia and Novozelandic (Fig. 3), providing areas with important natural laboratories for better understanding biotic responses to trajectories of future climate change.

These rapid warming events had profound impacts on 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, with some experiencing population bottlenecks and consequent losses of genetic diversity (16). Population decreases and extirpations were widespread in Eurasia and North America during the LD warming events, with accompanying shifts in species distributions and reorganisation of diversity patterns (41). For example, in Eurasia, the Woolly Mammoth (*Mammuthus primigenius*) retracted its range, surviving the 14.7 warming event in cool refugia (42), while the Arctic Fox (*Alopex lagopus*) was unable to track habitat shifts associated with LD warming events in mid-latitude Europe, leading to its regional extinction (43). In North America, species evenness of small-mammal communities decreased sharply in response to rapid warming, negatively

affecting functional stability and community persistence (44); and a widespread and regionally abundant tree species, *Picea critchfieldii*, underwent extinction (45).

These alterations in species' distributions and abundances radically changed the structure and function of ecosystems, influencing the physical formation of habitats, geochemical cycles and the productivity of ecosystems (46, 47). 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 (48). Moreover, decreases in the ranges and abundances of terrestrial megafauna reduced the contribution of these animals to nutrient cycling and redistribution (47), with consequences for structure and function of ecosystems (49). Late-glacial population decline of megaherbivores in the North American interior reduced browsing pressure on broadleaved trees, facilitating a rapid transition from coniferous forest to mixed coniferous-deciduous forest, along with a change in fire regime (46).

Climate-driven biodiversity dynamics in real time

Environmental policy, 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 many opportunities, particularly in the Holocene (from ~ 10 ka to the present), to examine climate–biodiversity dynamics at the taxonomic and spatiotemporal scales used by decision-makers. High resolution Holocene paleoclimate reconstructions show that extreme climate anomalies often cluster together, forming droughts and pluvial periods, with nonstationary durations, return frequencies and magnitudes (50). These episodic climate events drive ecological responses at different temporal and spatial scales, shaping species' ranges (51). For example, colonization via long-distance dispersal for some North America plants during the Holocene, was contingent on decadal-scale climate variation, while establishment was followed by backfilling during extended favourable climate episodes (52). Under this ratchet-like expansion, potentially suitable habitat remained unoccupied for centuries or longer, until a sufficient number of expansion episodes accumulated to permit population establishment, expansion, and backfilling (51). Patterns of these distribution shifts are partly contingent on species' life-history traits, with smaller temporal lags expected for short-lived highly mobile species (53).

Paleo-records from the Holocene also show that landscape structure and cross-scale variation in seasonal-to-decadal climate fluctuations govern population declines and extirpations in established areas of species' ranges; and that population declines are not necessarily accompanied by changes in geographic distribution (54), as is often assumed in conservation assessments (55). For example, a rapid population increase of eastern Hemlock (*Tsuga canadensis*) occurred near its western range margin in the late Holocene, but with no accompanying geographic expansion (56). While, its geographic range held steady during a dramatic range-wide population decline in the mid-Holocene (57). By providing important new perspectives on how cross-scale climate variation regulate natural populations, high-resolution paleo-archives from the Holocene are improving knowledge and strategies for protecting biodiversity (52).

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 distant and recent contemporary trends in local-to-global 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 deriving conservation policies (58). However, to date, their temporal focus has been limited (59).

Paleo-archives provide opportunities to quantify EBVs under a far wider range of climatic and environmental conditions, including paleo-enabled EBVs measured at the population, species, community and ecosystem levels (16, 44). The application of EBVs to paleo-data makes the direct utilization of past biodiversity responses in future environmental management more straightforward, since EBVs are quickly becoming the common currency for reporting biodiversity change to the scientific and policy communities (59, 60). Technological advances that allow changes in allelic diversity to be uncovered from ancient genomes (61) are likely to provide an additional and important class of paleo-enabled EBV (‘genetic composition’) for assessing the climate-sensitivity and threat status of different taxa (58).

Species distributions and abundance

Species abundance is an EBV that can be inferred from diverse fossil records (morphological, molecular, or both) or from genes in extant populations, 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 (41, 62), making paleo data more comparable to ecological abundance-based indicators of biodiversity change upon which present-day conservation policies are based [Living Planet Index, IUCN Red List and IUCN Green List], and targets to reduce biodiversity loss assessed [Convention on Biological Diversity (CBD)] (9, 17, 63). Given that warning signals of biotic transitions or state-shifts are commonly identified using time-series abundance data (64), paleo-archives provide opportunities to improve knowledge of critical thresholds that signal population collapses, possible extinction events and ecosystem shifts in response to large-magnitude climate shifts (65). Moreover, a deeper-time perspective enables natural variability bounds in species abundances and other EBVs to be estimated over large-scale climate 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 real declines from greenhouse gas warming and other human-environment interactions are being prioritized (20).

Changes in patterns of spatial distributions of species is another EBV that can be inferred from the fossil record and used to monitor single or aggregated taxonomic units during periods of late Quaternary climate change, enabling paleo-data directly to inform 21st Century conservation decision making, through an improved understanding of indigenous distributions and the role climate had in past range contractions and expansions (Fig. 4). If biodiversity-threat metrics are generated over long time periods using paleo-data, the time period for conservation assessments can be extended back well before written records. Furthermore, paleo-enabled EBVs allow morphological changes within species populations to be measured across time (Fig. 4), providing a deeper understanding of species-level responses to global change (60) and an improved capacity to detect ecological regime shifts (66).

Assessments of biodiversity values are strongly dependent on the spatial and temporal scale of their evaluation which, in turn, influences conservation-planning decisions (67).

Indeed, using 1500 CE as a baseline for vulnerability assessments (68) risks overlooking past range shifts, population collapses and the erosion of genetic diversity. This can have direct bearing on evaluations of conservation status (IUCN Red List) and measures of conservation success (IUCN Green List) (17). A daunting 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 models to improve theories and make generalities regarding the spatial dynamics of range collapses of species (6-8). For example, a common view in conservation is that densities in peripheral populations are typically lower and less stable than at the centre of a species' range (55), 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 many species whose persistence may depend upon populations close to the periphery of their historical ranges (according to paleo-archives) (69). Inferences of range shifts during the late Quaternary provide unique opportunities to develop an improved theory of population declines (67), allowing for direct tests of whether geographic ranges collapse first along the periphery and are thereafter lost from the interior of a species' historic range, or *vice versa*.

Communities and ecosystems

Conservation goals are shifting from those focused on preserving current spatial patterns of species toward goals that focus on maintaining ecological and evolutionary mechanisms that are fundamental for sustaining ecosystem function in the long term (70). Environmental DNA provides a powerful new source of data for establishing the temporal dynamics of communities and ecosystems across hundreds to thousands of years, providing a promising route for quantifying how resistant an ecosystem service is to climate induced perturbations (and other external factors), and the recovery times following an episode of degradation (71). Accordingly, metagenomics data can be mined for aDNA (72), and the resulting information used to calculate "biodiversity intactness" (73), which today is used to guide policies for reducing future biodiversity loss (63). This is done by quantifying change in the diversity of a wide assortment of organisms in a given geographical area, following a climatic shift or other environmental disturbance. Furthermore, paleo-data can yield insights into the relative roles of biotic and abiotic controls on ecosystem properties, including nutrient cycling (48), NPP and plant biomass (Fig. 4) over periods of stability and disturbance. These paleo-enabled

measures of ecosystem function are important for determining thresholds for ecosystem collapse and designing effective protocols for assessing ecosystem-level threat status under climate change (74).

Processes that regulate climate-biodiversity dynamics

The challenge of synthesizing disparate evidence from paleo-archives, to make generalizations on which species and ecosystems are most at threat from future climate change, and what their losses would mean to human wellbeing, is being addressed using process-based (theory- and data-driven) simulation models. These approaches, which run at high-resolution temporal and spatial scales and across large geographical extents, can offer unique insights into climate–biodiversity dynamics during the late Quaternary (75). They can be used to infer causality, making them particularly suitable for guiding decisions regarding the pace of change and desired states of ecological systems (76).

These mechanistic approaches are increasingly useful for assessment of the relative importance of ecological and evolutionary responses to different spatiotemporal scales of past climate and environmental change in shaping different levels of biological organization (Fig. 5). Driver–state relationships that can now be simulated include the effect of climate change on migration, adaptation, extinction and speciation, however, the number and combination of processes simulated, depends on the spatial scale and unit of biological organization being modelled (Fig. 5) Such simulations, which unpack complex patterns of biodiversity, driven by multiple biological processes and agents, enable dynamical responses to environmental change to be better contextualized and so integrated into future biodiversity management (7).

Process-based models also permit *in silico* experiments on the biological consequences of rates of past climate and environmental change, allowing counterfactual hypotheses of eco-evolutionary dynamics to be tested (77). Model parameters can be held constant to understand the isolated and/or interactive effects of other dynamical processes on emergent patterns (78). Detailed scenario comparisons have been used to investigate competing explanations for ecological regime shifts in Australia during the late Holocene (79), migration patterns of anatomically-modern humans over the past 125,000 years (80), and extirpation patterns in Eurasia during the Pleistocene-Holocene transition (81). Application of pattern-orientated modelling (POM) in evaluating and calibrating models of complex paleoecological systems has been the key to testing many hypotheses and counterfactual arguments. In this context, spatio-temporal patterns inferred from the paleo-record are

used as filters for evaluating whether a model is adequate in its structure and parameterisation to simulate the underlying mechanisms (82). A requirement of POM is that its state variables are expressed in equivalent units to targets 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 parameterisation) for conservation management, providing novel opportunities to test and improve early-warning systems that signal impending population collapse, extinction or ecosystem shifts (7).

Looking ahead

Climatologists are taking full advantage of the long-term history of the planet, recorded in paleo-archives, to understand mechanisms of climate change, quantify trends, and develop scenarios of future climate change (14). A wider usage of paleo-data for quantifying and reporting climate-biodiversity dynamics, particularly in regions where past and future climate change is likely to be similar (Fig. 3), will require an expansion of the taxonomic, spatial and temporal extent of current paleo-archives. Large-scale shotgun sequencing of biological remains preserved in the permafrost, ice-cores, or marine and lake deposits can provide cost-effective solutions for increasing the taxonomic coverage of paleo-samples beyond the level of genera, often improving knowledge of the geographical distribution of species and ecological communities (83). An expansion of paleoecological information in open-access global databases, including georeferenced ancient DNA, will further increase the geographical representation and temporal coverage of paleo-enabled conservation metrics (84).

Methods for extending the temporal coverage of past climate-biodiversity dynamics beyond the 50ky age-limit of radiocarbon dating include, Uranium/Thorium dating, optically stimulated luminescence, paleo-magnetism, and infrared stimulated luminescence (85). However, dates for climatic and biotic events derived from these approaches are not, generally, resolved at human-relevant time scales, limiting the assignment of ecological shifts to rapid climatic change beyond 50ky. Tephra layers from volcanic activity, preserved in ice cores and stalagmites, have the potential to align paleo-environmental proxies in space and time for the LD, and earlier, making them particularly useful for understanding biodiversity

and ecosystem responses to regional climate change (86). Because individual paleo-climate proxies only approximate broader-scale changes in climatic conditions (24, 87), a more detailed understanding of the paleoecology of species and their ecosystems will result from initiatives to improve the spatiotemporal resolution of paleoclimate projections from multiple earth-systems models, using continuous simulations of the transient climate, that extend beyond the LD. 1-2 lines from Bette on the state of play

While, high-throughput DNA sequencing technologies can generate genetic-based measures of extinction risk (inbreeding coefficient and mutational load) and adaptive potential to climate change (allelic diversity), they have been primarily applied to contemporary or 20th century samples (88). However, genomic information extracted from well-preserved fossils is now allowing changes in genetic diversity to be estimated across extended time periods (back at least LD) (89, 90), informing ecological research on climate change susceptibility, providing important pre-industrial baseline genomic information for conservation programs, including genetic rescue (91). Aligning population-level genomic information on inbreeding and connectivity (F_{st}) from ancient samples (61) with improved paleo-environmental proxies, will provide important opportunities to better understand magnitudes and rates of change in genetic-based conservation metrics under climate change.

Decreased costs of recovering endogenous DNA from fossils for generating genomic information is facilitating the compilation of more robust and taxonomically diverse data sets (92). This is likely to improve knowledge of how gene function and gene expression regulate the abilities and speeds at which *in situ* populations adapt to different rates and magnitudes of climate change, making the inclusion of genomic adaptation in conservation schemes and metrics soon feasible. Indirect paleogenomics evidence suggests a strong potential for fast genomic adaptation to rapid climate change (93). However, the generality of these findings (and their potential relevance to abrupt warming events) is unknown, given that they are based on a single taxa and small sample sizes.

Simulation and advanced empirical approaches that compare mechanisms of change in nearby regions with different histories of colonisation 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 in Madagascar and New Zealand did not occur until the first millennium of the Common Era (94, 95). Detailed comparisons of long-term biodiversity and

ecosystem change on these islands, with those on continental Africa and Australia (both with long human histories), could prove enlightening.

Strategies for 21st-century environmental management necessitate 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 rapid warming events can be followed *in situ*, using cross-disciplinary approaches, providing cost-effective and scalable solutions for species' conservation and the maintenance of resilient ecosystems in many bioregions of the world. This will assist in halting climate-driven biodiversity change in the 21st century and beyond.

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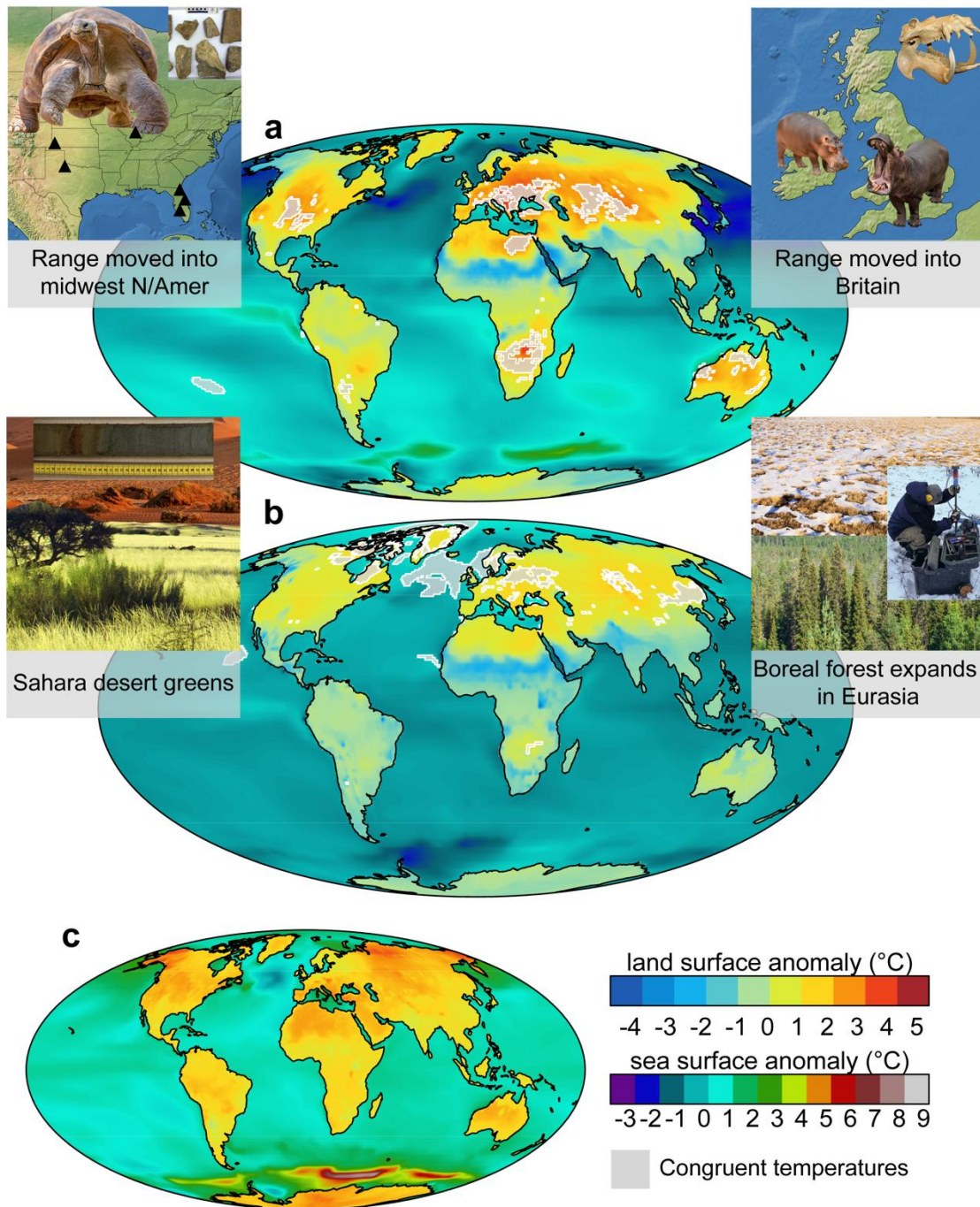


Figure 1: Congruence between warm periods of the late Quaternary and near-term forecasts. Maps of Boreal summer (JJA) land and sea-surface temperature anomalies from pre-industrial conditions during the last interglacial (~127ka; **a**), mid-Holocene (~6ka; **b**), and the near future under Representative Concentration Pathway 4.5 (2030; **c**). White areas in **a** and **b**, highlight areas that are congruent with the anomalies for **c**. Climate simulations are described in the Supplementary material.

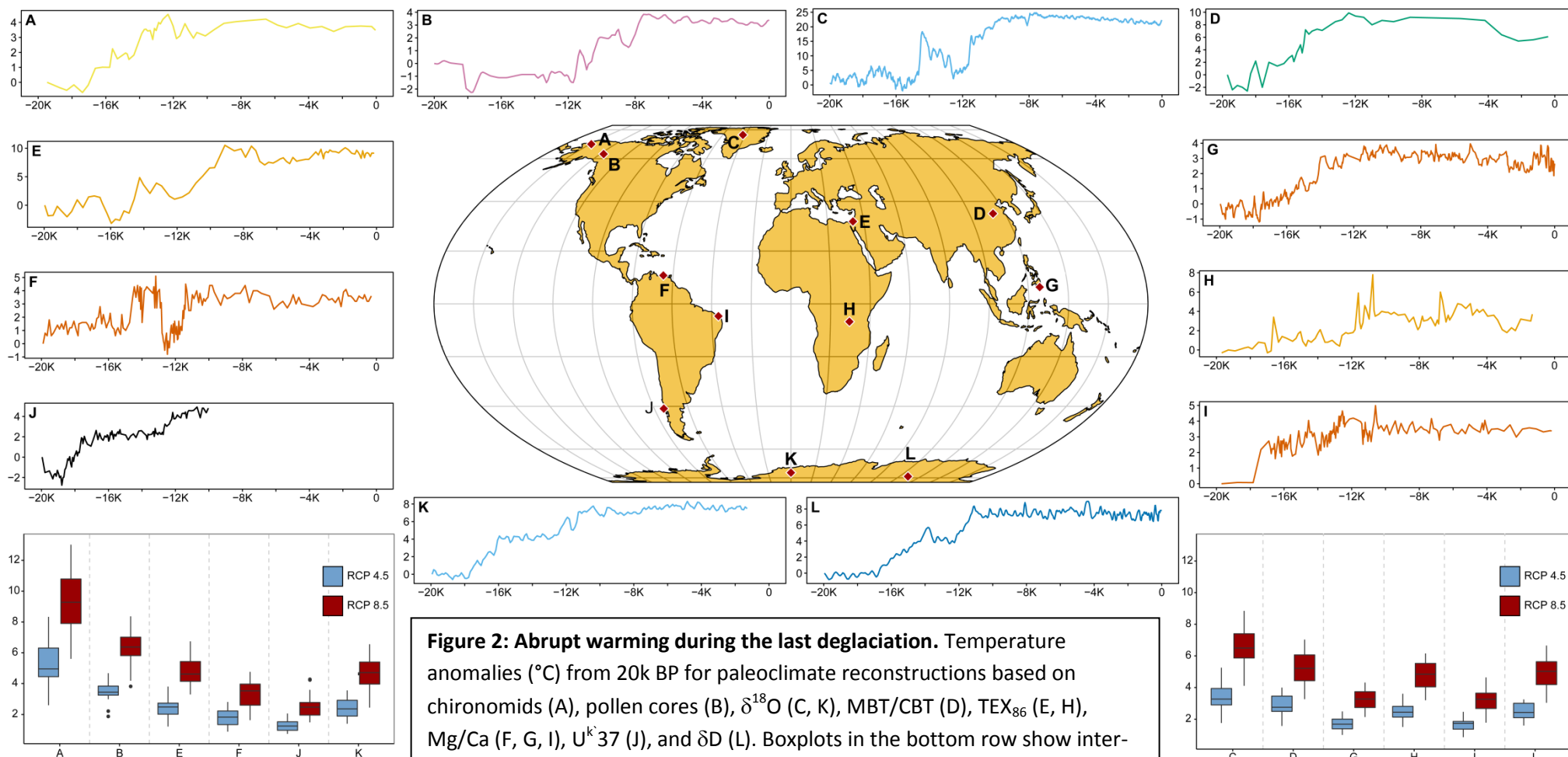


Figure 2: Abrupt warming during the last deglaciation. Temperature anomalies (°C) from 20k BP for paleoclimate reconstructions based on chironomids (A), pollen cores (B), $\delta^{18}\text{O}$ (C, K), MBT/CBT (D), TEX_{86} (E, H), Mg/Ca (F, G, I), $\text{U}^{\text{k}}37$ (J), and δD (L). Boxplots in the bottom row show inter-model (n = 18) variability in forecast temperature change in 2090 from a 20-year baseline focused on 1990, under two greenhouse gas emission scenarios. See Supplementary Material for further information.

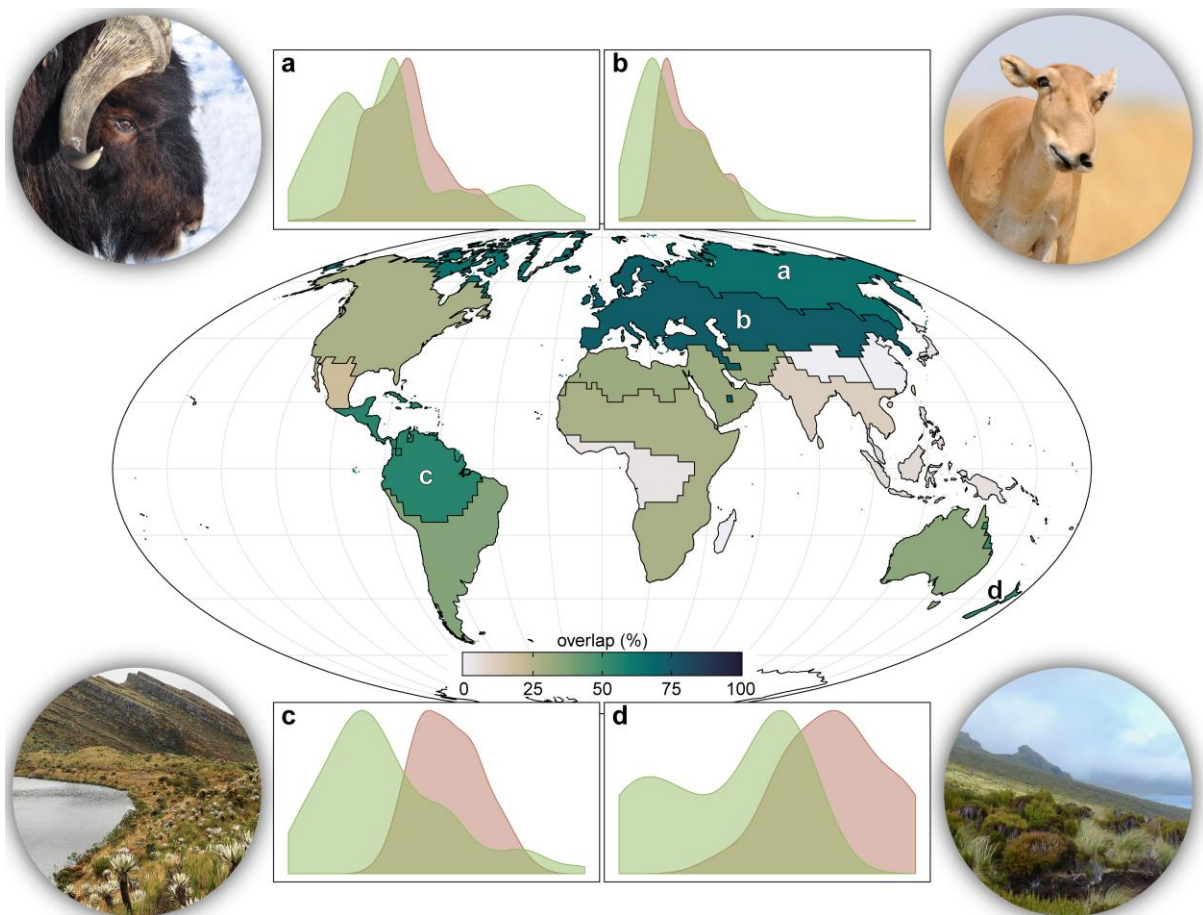


Figure 3: Percent overlap in past and future abrupt warming in Zoogeographic regions. Map of percent overlap between kernel density estimates (KDE) of near-century temperature change during periods of rapid global-mean warming through the LG; and under an RCP 8.5 scenario based on Brown et al. 2019 (13). The inserted plots show selected KDEs and species and ecosystems sensitive to climate change for the Arctic-Siberia (a), Eurasia (b), Novozelandic (c) and Amazonia (d). Past KDE plots in green and future plots in red. Percentage overlap: 64% (a), 72 % (b), 55% (c) and 52% (d). See Supplementary Material.

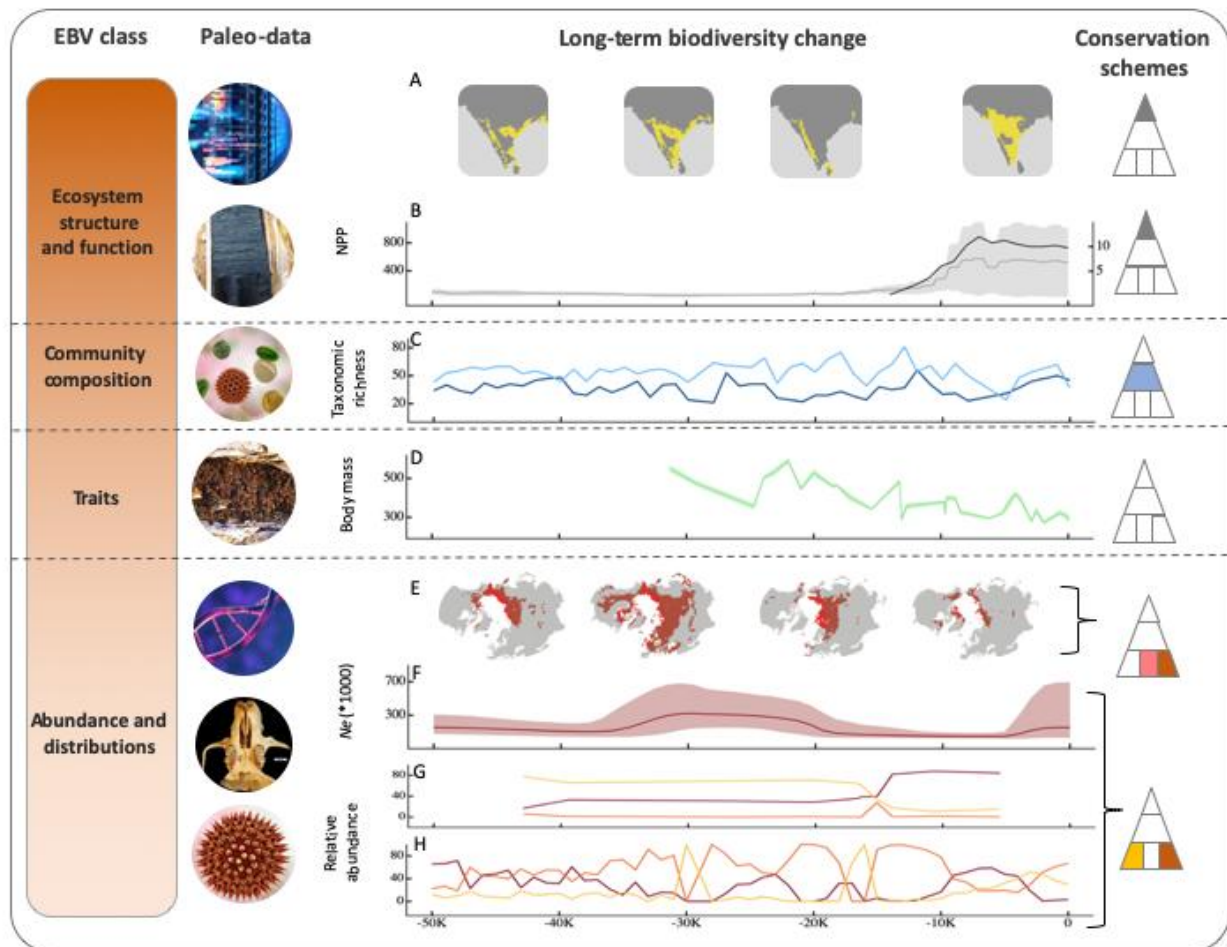


Fig.3. Paleo-enabled EBVs inform conservation schemes. (A) Savanna ecosystem, India; (B) Net primary productivity, North America (grey), and biomass (black), eastern Canada; (C) Taxonomic richness of plants in south Italy (blue) and Guatemala (light blue); (D) Woodrat body mass, Great Basin US; (E) Modelled distribution of musk ox; (F) Estimated population size of musk ox; (G) Mammal relative abundance, southern Australia (*Pseudomys australis* [red], *Rattus fuscipes* [orange], *Pseudomys apodemoides* [yellow]) (H) Plant relative abundance, southern Italy (*Albies alba* [red], *Fagus sylvatica* [orange], *Carpinus betulus* [orange]). Conservation schemes: IUCN Red List Ecosystems (grey), Biodiversity Intactness (blue), Living Planet Index (yellow), IUCN Red List (red) and Green List (pink). See Supplementary Material.

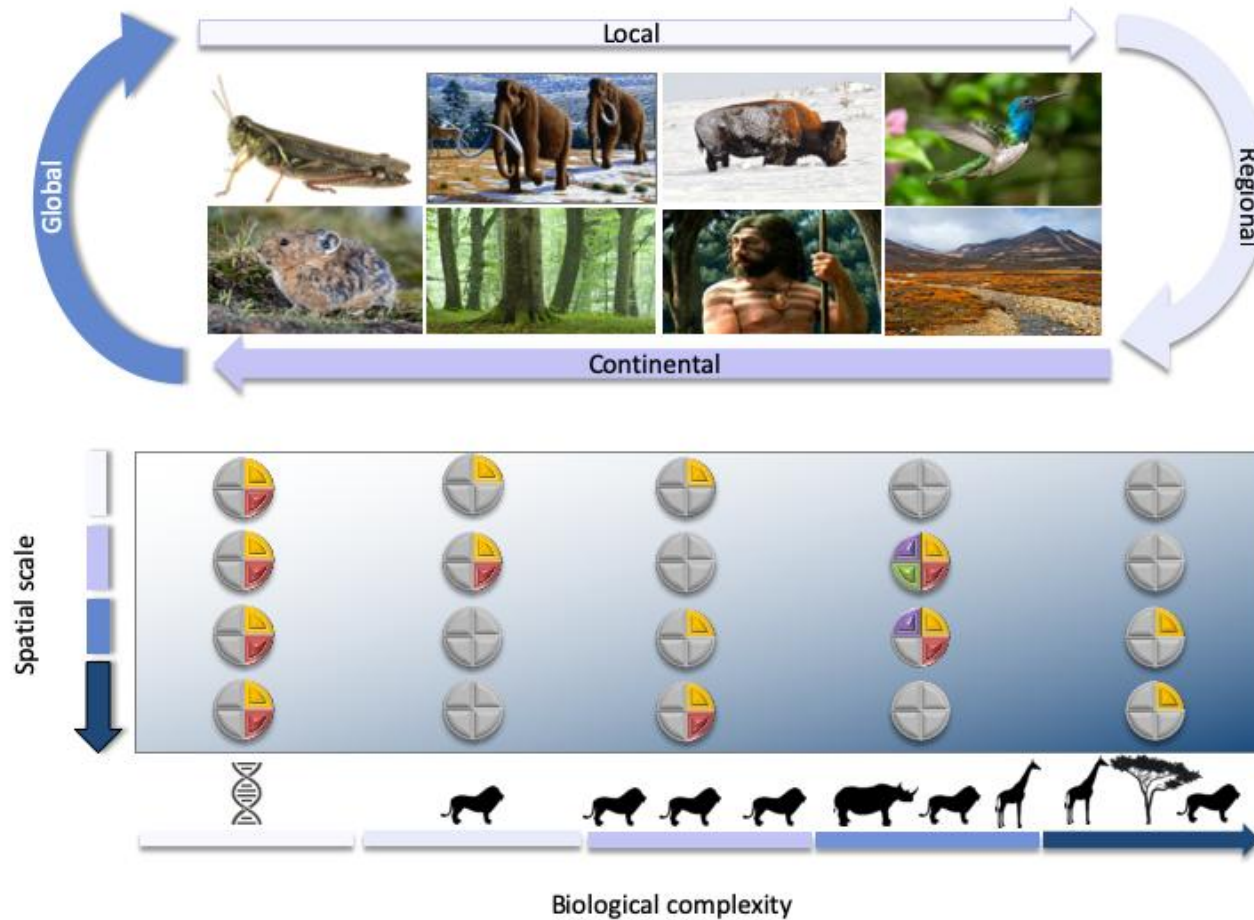


Figure 5: Simulating mechanisms of past climate-biodiversity dynamics. Process-explicit models can be built across different levels of biological organisation (gene, individual, population, community and ecosystem) and spatial scales (local, regional, continental and global). Pie charts show ecological and evolutionary processes that have been modelled at different biological and spatial scales: mortality (yellow), movement (red), adaptation (green) and speciation (purple). See Supplementary Material.