

Review

Cracking the Code of Biodiversity Responses to Past Climate Change

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How individual species and entire ecosystems will respond to future climate change are among the most pressing questions facing ecologists. Past biodiversity dynamics recorded in the paleoecological archives show a broad array of responses, yet significant knowledge gaps remain. In particular, the relative roles of evolutionary adaptation, phenotypic plasticity, and dispersal in promoting survival during times of climate change have yet to be clarified. Investigating the paleo-archives offers great opportunities to understand biodiversity responses to future climate change. In this review we discuss the mechanisms by which biodiversity responds to environmental change, and identify gaps of knowledge on the role of range shifts and tolerance. We also outline approaches at the intersection of paleoecology, genomics, experiments, and predictive models that will elucidate the processes by which species have survived past climatic changes and enhance predictions of future changes in biological diversity.

Looking to the Past to Understand the Future of Biodiversity

Current estimates predict that atmospheric CO₂ levels may rise up to 450–500 ppm by the end of this century, potentially driving an increase in global average temperature on the order of 2–5°C [1]. These projected magnitudes and rates of future climate change, unparalleled in many million years [2], pose major threats to biodiversity [3–6]. The scientific community is struggling to fully comprehend the range of responses of biodiversity to climate change, to anticipate whether species can respond quickly enough, and to pinpoint the various roles of life-history properties [e.g., dispersal capacity, genetic diversity, reproductive strategies, **phenotypic plasticity** (see [Glossary](#)), population growth rates] in adapting to a changing environment. In order to make reliable predictions it is essential to advance our understanding of the underlying principles and mechanisms of biodiversity responses. One fruitful approach is to look to the past by using geohistorical records to learn how individuals, populations, communities, and biomes have responded to previous climatic changes ([Box 1](#)) [7–11]. Whether individuals and populations will adapt by evolutionary change or plasticity, whether they will migrate fast enough, and whether those responses will be adequate to forestall collapses of species ranges and prevent widespread species extinctions can be explored using case studies from the past. Indeed, past climate change, whether abrupt or gradual, and whether occurring in deep time or recent history, offers a vast set of unplanned natural experiments to explore biodiversity responses and test ecological and evolutionary theories. Recent years have seen the accumulation of well-documented examples of the influence of climate change on persistence, adaptation and diversification, dispersal, and extinction (e.g., [12–15]). The effects of climate change on rates and routes of range shifts have been intensively studied by biogeographers and paleoecologists, augmented recently by molecular markers and ancient DNA (aDNA; [16, 17]). *In situ* tolerance to changing climate conditions has been explored in the

Highlights

The study of biodiversity responses to past climate change can greatly help us understand current threats and forecast future responses.

There is ample evidence of effective migration, *in situ* tolerance, and adaptation in response to past climate changes. But there is also evidence of widespread extinctions.

The unprecedented nature of modern global change greatly complicates prediction. Large uncertainties remain about the expected rates of migration and evolutionary adaptation, or the role of phenotypic plasticity in avoiding extinction.

Integrative research programmes combining paleorecords (e.g., fossils, ancient genomics) with mechanistic models and experiments (e.g., resurrection experiments) hold great promise to improve our understanding and predictive ability.

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fossil record using functional morphology and evolutionary genetics, including recent experimental approaches like ‘resurrection ecology’ [15,18,19]. Finally, paleoecological records of local and global extinctions provide information on the nature and consequences of the failure of *in situ* tolerance and range shifts [20,21].

However, key knowledge gaps remain. The relative importance of different mechanisms involved in species tolerance (e.g., evolutionary adaptive change versus phenotypic plasticity), and the nature and rates of climate-driven anagenetic evolution (a transition of one species to another) and cladogenetic evolution (the separation of a species into two or more species or clades) remain poorly understood [22]. The relative efficacy of *in situ* tolerance and range shifting under different rates and magnitudes of climate change is obscure [23,24]. Although much attention has been devoted to paleoecological records of species’ range shifts [25], the speed and underlying controls are not clear except in a few specific cases [24]. Moreover, significant challenges remain for better integrating knowledge, scales, methods, and data from a variety of biological disciplines, from paleoecology to genomics. In this review, we (i) synthesize the main responses of biodiversity to past climate change from deep to recent time (tolerance *in situ*, range shifts, and their simultaneous failure, resulting in extinction); (ii) identify key knowledge gaps concerning underlying mechanisms (which span a broad set of biological disciplines); and (iii) review and discuss new approaches that integrate multiple methods and disciplines to better understand the strategies by which life adapts to climate change and to better anticipate future responses of biological diversity.

Biodiversity Responses to Climate Change

Tolerance, Adaptive Evolution, and Diversification

Biotic responses to climatic and environmental changes as shown by the fossil records vary from macroevolutionary divergences (at very long (10^6 – 10^7 year) time scales), to **adaptive evolution** (10^0 – 10^5 year), to phenotypic adjustments in place (10^{-1} – 10^3 year). Long-term climate change has been considered an important driver of high-order diversification, as clades respond to new climatic regimes [14]. In shorter time spans, many individuals and populations (e.g., long-lived modular organisms like corals and plant genets) can tolerate a high degree of climate change *in situ*. Paleogenetic records also suggest that adaptive evolution can support long-term persistence of species in response to climate change [26]. Adaptations can enable exploitation of new niches: for example, adaptive mutations in woolly mammoth haemoglobin allowed the exploitation of high-latitude cold environments during the Pleistocene [27]. Examples of more recent microevolutionary responses to climatic change include changes in the body colour of owls during warmer winters [28], or adaptive changes in the flowering time of *Brassicacae* in response to drought [29].

Whether adaptive evolutionary change or plasticity are the prevalent strategy to tolerate climatic changes *in situ*, and at what spatial and time scale these two processes play a role, can be difficult to disentangle for extant populations [22,30] and are even more challenging for ancient extinct populations; however, both are candidate processes in population persistence under climate change. For most reported cases of climate-driven phenotypic changes in the wild, it remains unclear whether they are caused by microevolution or phenotypic plasticity, although recent meta-analyses suggest that most responses to climatic change are mediated by phenotypic plasticity [22,31] (see also [32–35]).

Range Shifts

Range shifting (usually referred as **migration** in paleo-disciplines) has been a dominant response of species to climate shifts in the past [25]. Past range shifts are typically inferred

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Box 1. Biodiversity Responses to Past Climate Change

Countless individuals in thousands of species across the globe will need to tolerate climate change *in situ*, disperse to more suitable climatic conditions, or undergo extinction. Figure 1 highlights a number of biodiversity responses directly or indirectly linked to climatic changes along the Cenozoic (past 66 million years). (i) During the Paleocene-Eocene Thermal Maximum (~56 million years before present) there were large extinctions in some marine groups (benthic foraminifera), remarkable poleward range shifts in others (dinoflagellates, mammals, reptiles, plants), and high community turnover [97]. (ii) Under a global cooling trend, winters became $>4^{\circ}\text{C}$ colder across the Eocene-Oligocene boundary, partially driving extinction of many terrestrial mammals in Europe as well as marine invertebrates globally [98]. (iii) Many thermophilous plants shifted their ranges southward and finally went extinct in Europe during the late Miocene global cooling [99]. (iv) More than half (52%) of the cool-temperate European tree genera did not survive the glaciation cycles starting at the end of the Pliocene [100]. (v) An adaptive mutation of haemoglobin enabled mammoths to tolerate the very low temperatures at high latitudes [27]. (vi) More than 70% of megafauna genera in the Americas and Australia, and 40% in Eurasia, underwent extinction within a relatively brief period of time (5000–10 000 years) in co-occurrence with climatic changes and human impacts [55]. (vii) Plants in North America migrated northwards between 450 and 2200 km in $<10\,000$ years under a warming of 5° [101]. Past temperature data from [102]; future temperature projections (under two greenhouse concentration scenarios: RCP2.5, most benign, and RCP8.6, most extreme) from [1].

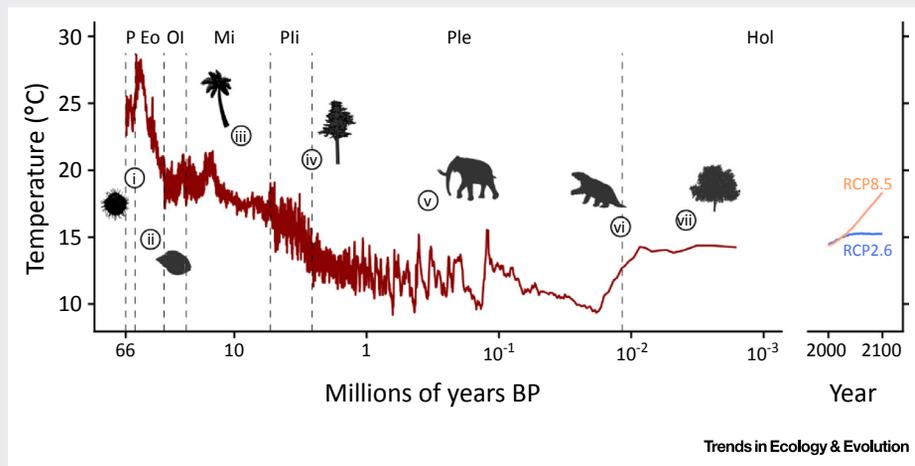


Figure 1. Future Climate Forcing will Surpass those of the Previous Several Million Years [2]. Abbreviations: Eo, Eocene, Hol, Holocene; Mi, Miocene, Ol, Oligocene, P, Palaeocene, Pli, Pliocene, Ple, Pleistocene.

from spatial and temporal patterns in fossil data [36,37], geographic patterns in genetic markers of extant and extinct populations [17], or both (e.g., [38]). They have shown variable species-specific spatial trajectories, timing, and migration rates, ranging from a few tens to a few thousand m/year, with averages around 2.7 km/decade [39–41]. Overall, there is evidence of both rapid range shifts and community reshuffling [42] as well as many species lagging behind climate [43], which reinforces the high specificity of range shift patterns across taxa.

There are many different mechanisms by which climate change influences range shifts [44]. First, climate change can improve suitability beyond the range limit so that species may establish at formerly unsuitable areas like higher latitudes or altitudes [45,46]. Second, climate change could foster colonisation of new areas in several ways: enhanced fecundity of source populations (thus increasing propagule pressure), increased propensity to disperse or emigrate (particularly in animals), or acceleration of dispersal processes [47,48]. Climate change can also enhance establishment of propagules after arrival, both directly [49] and – particularly in rapid climate change – by reducing populations of dominant species via mortality or disturbance [50]. Finally, climate change could reduce the probability of the extinction of leading edge populations, for instance due to extreme climatic events [51]. A variety of processes are

Glossary

Adaptive evolution: results from the propagation of advantageous alleles in populations through natural selection, driven by environmental selection pressure acting on genes underlying species traits linked to fitness.

Dormant propagules: a still living seed, cyst, spore, or egg that has arrested development and is preserved in ice, soil, sediment, permafrost.

Experimental paleoecology: experimental studies to test sufficiency and necessity of mechanisms (or combinations or sequences of mechanisms) invoked to explain paleoecological phenomena.

Migration: spatial displacement of organisms leading to shifts of species distributions.

Paleogenomics: the study of ancient genomes to reveal functional genetic patterns through time, supporting inferences concerning evolutionary adaptation, functional traits, population dynamics, domestication, genetic events preceding extirpations or extinctions, and other patterns of interest.

Phenotypic plasticity: ability of individuals of a genotype to alter physiology, morphology, anatomy, phenology, behaviour, or other phenotypic traits in response to environmental change.

Resurrection ecology: study of traits and environmental responses of past populations by hatching or germination of dormant propagules and culturing or cultivation of the organisms.

Process-based models: spatially explicit approaches that simulate the effect of climate and environmental conditions on important vital rates (including population growth, dispersal, and plasticity in demographic traits) to explain species distributions and their changes, including range shifts and local extirpations.

Tolerance: ability of a population to persist at a site under environmental change by adaptive evolution, phenotypic plasticity, or both.

involved in species' range shifts, all of which can be directly or indirectly (e.g., mediated by species interactions) influenced by climate change [23,50,52,53]. A challenge for ecologists, biogeographers, and paleoecologists is to identify generalizations and to understand the role of species-specific, locale-specific, and time-specific contingencies and idiosyncrasies in driving patterns and rates of range shifts.

Extinction

When species cannot tolerate climate change *in situ*, or colonize suitable habitat elsewhere quickly enough, they become extinct. In extreme cases, many high-order clades can be lost in mass extinction events [54,55]. There is strong support for a primary role of climate change, alone or in connection to other factors, in extinction events of different magnitude over the past 500 million years, including the recent extinction of large mammals in the past 50 000 years [21]. Evidence of climate-driven species extinctions in recent centuries is limited [56], with rare exceptions being synergistic functions of both 20th century human-induced climate change and other proximate drivers of extinction (including infectious diseases) [57]. However, anthropogenic climate disruption is predicted to soon compete with habitat destruction as the most important driver of contemporary extinctions [58,59].

Climate change may trigger extinctions and local extirpations by surpassing the physiological limits of species, by reducing primary productivity of ecosystems and thereby local population fitness across food webs, and indirectly by disrupting ecological interactions via changes in species distributions or phenology. For instance, coral bleaching, the loss of intracellular endosymbionts due to the increase in prevalence of extreme heating episodes and changes in the carbon cycle, is one of the main supported mechanisms behind coral extinctions during the five mass extinction events [60]. Also, drier and colder climatic conditions during the Last Glacial Maximum triggered a reduction in overall primary productivity, provoking losses in genetic diversity and populations of large grazers [13], depleting lineages (e.g., bowhead whales) [61], and contributing to local and global extinctions [21]. These pathways to extinctions in different periods of the Earth's history share some commonalities. In particular, climatic changes that exceed in magnitude and speed those experienced during the evolutionary history of species usually trigger extinction events, and climate change has frequently interacted with other extinction drivers [61].

Unknowns, Challenges, and Routes Ahead

Our review of the modal responses of biodiversity to past climate change unveils key knowledge gaps concerning the underlying mechanisms. We identify and discuss them in this review and propose new integrative approaches that show potential to crack the code of how biodiversity responds to climate change.

Evolutionary Adaptation versus Plasticity?

Climate-relevant decisions and policies implemented today (e.g., levels of CO₂ emissions) have both short- and long-term consequences for future biodiversity, influencing range shifts, divergence, speciation, hybridization, anagenetic evolution, and extinction. Paleo-archives reveal that speciation, evolution, and phenotypic change have played roles in species responses to past environmental changes. However, the relative roles of those mechanisms in different settings, for different taxa, and across different timespans need clarification and exploration [62].

At deep-time scales, comparative phylogenetics and novel macroevolutionary approaches are offering new insights into speciation and phenotypic change in response to major climatic shifts

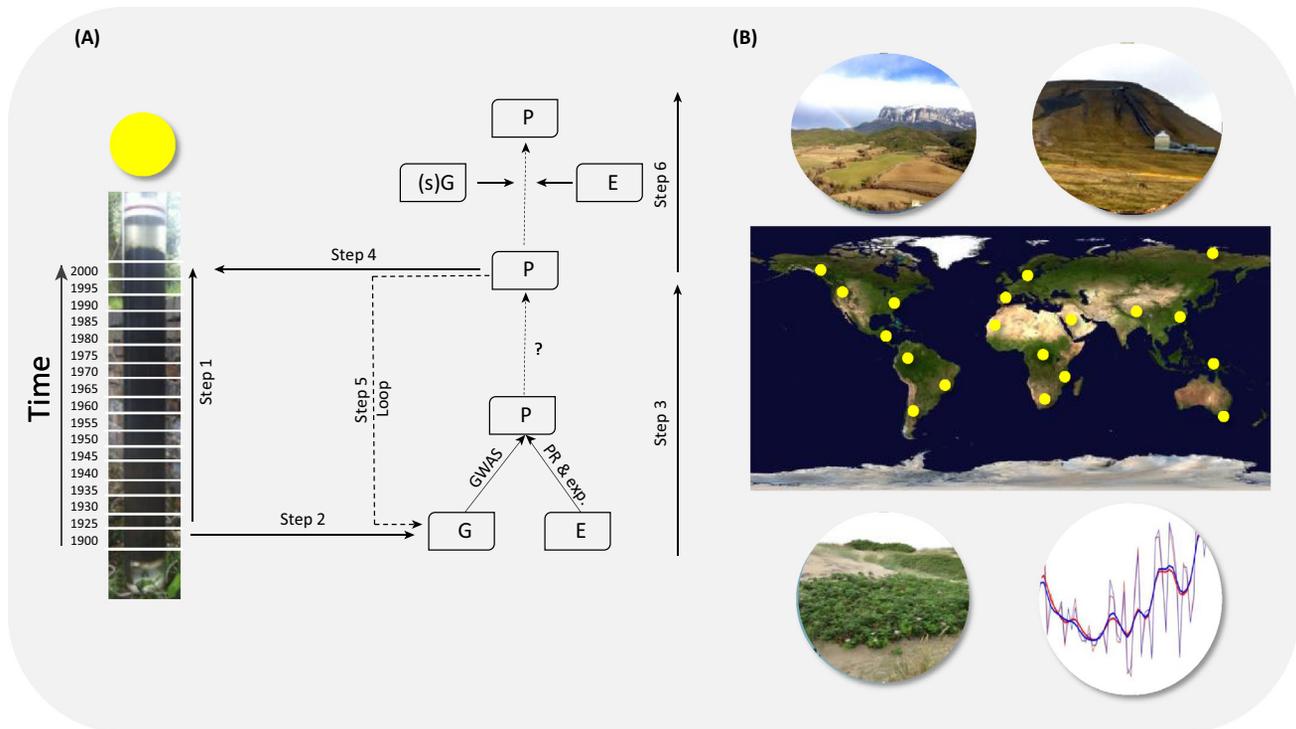
[63]. For instance, it was found that expected future climate change largely surpass past rates of climatic niche evolution among vertebrate species [64]. Comparative approaches allow fitting various models of phenotypic evolution and diversification to phylogenies in order to estimate evolutionary rates, including speciation and extinction [14]. Recently, models that can explicitly test for the effect of climatic changes on these evolutionary rates have been developed [65–68]. Future studies including genomic level data across thousands of species and climate-dependent evolutionary models will provide deeper insights into the role of climate change on speciation, including bursts and phenotypic change.

At shorter time spans, from thousands to hundreds of years, comparative analyses of species and populations provide important insights into the evolutionary processes that led to present day genetic and phenotypic diversity. However, when limited to exploring extant genetic patterns, inferences on past processes can be limited. New approaches considering species' traits and explicit scenarios of past range dynamics can bring much deeper insights on the role of phenotypic variation on population persistence, range shifts, and generation of genetic structure [69]. Alternatively, long-term observational studies enable measurement of evolutionary processes by comparing temporal changes in genetic and phenotypic diversity with expectations of neutral and adaptive evolutionary models [70]. Long-term studies, however, may require commitments beyond the career or life spans of individual researchers. **Resurrection ecology** (Figure 1 and see 'Anticipating Extinctions' section) provides an alternative and complementary path to reconstructing long-term patterns of evolutionary changes and unravelling mechanisms of response to climatic and other environmental changes [15].

Migrating Fast Enough?

Although dispersal is a key process underlying range shifts and the spread of native and invasive species, the migration capacity of species under rapid climate change remains uncertain [23]. While some taxa seem unable to shift ranges under changing climates [43], others seem able to migrate at a fast pace [45]. Attempts to explain observed range shifts based on species traits or ecological strategies have obtained modest results [71,72] (but see [73]). Low predictability may be expected given the large number of processes involved in range shifts, as well as the complexity and path-dependence when those processes interact. The dispersal process itself is highly stochastic and inherently uncertain [74]. Other important processes include size and fecundity of source populations (which determine propagule pressure), gene flow, local adaptation, evolution of dispersal, biotic interactions (competition, facilitation, mutualisms), Allee effects, and so on, all of which are likely to be affected by climate change [23]. Spatial heterogeneity on the landscape plays a role (e.g., dispersal-target size), as does high-frequency climate variability [47,50]. As a result, we may not be able to go much farther than estimating dispersal potentials for different species or populations [74]. A critical challenge is to use paleoecological and ecological data to identify generalizations that can emerge from the location-, species-, and event-specific particulars of detailed case studies [47,50].

Paleoecology has largely contributed to estimate how fast species migrated under past climatic changes and under minimum levels of prehistoric global human intervention. Unfortunately, contemporaneous dispersal rates are likely to be rather different than past rates due to radically different conditions (e.g., more fragmented habitats, missing and novel interactions, or nearly unlimited human-mediated dispersal) [23]. Hence, estimates of past migrations rates, however informative, may be of limited value when attempting to forecast future range shifts. Instead, a better understanding of the causes of variation in range shift rates may move us forward. Comparative studies of range shifts patterns among tens or even hundreds of species could



Trends in Ecology & Evolution

Figure 1. Reconstructing Historical Patterns of Evolutionary Change for Unravelling Mechanisms of Genetic and Plastic Response to Anthropogenic Environmental Changes. (A) Conceptual framework for the integration of resurrection ecology and predictive models. Using for example *Daphnia*, **dormant propagules** can be resurrected (step 1). On resurrected propagules, genetic (G), and phenotypic changes (P) can be quantified over evolutionary time. Similarly, environmental factors (E) can be inferred from historical records or measured (e.g., via chemical analysis of sediment). The genetic mechanisms (G) underlying phenotypic changes (P) are identified via a genome-wide association analysis (GWAS) (step 2). The causal link between phenotypic changes (P) and environmental variation (E) is established via experiments with the support of historical environmental records or reconstruction of temporal trends in environmental variables (PR). The parameters for predictive models of phenotypic trajectories are trained on empirical data (G, P, and E) from the sedimentary archive (step 5). Several iterations may be needed to identify the parameters that best fit the empirical data. Using the optimized parameters, future trajectories of phenotypic (and the underlying genotypic) trajectories are identified, with a level of uncertainty (step 6). (B) Scaling up the approach described in (A) to a macroecological scale, across sites (represented by yellow circle) and biological systems within ecosystems from the tropics to the poles, we can identify evolutionary and plastic responses of species to global anthropogenic pressures (within circles from upper left to bottom right: land-use changes, habitat degradation invasive species, and climate change. Pictures sources: David Nogués-Bravo and Hans-Henrik Bruun).

throw some light into the role of environmental (contingent) factors as well as intrinsic factors that make some species migrate faster, slower, or not at all.

Anticipating Future Extinctions

Revealing how the accumulative failure of *in situ* tolerance and dispersal mechanisms leads to population extirpation and ultimately species extinction under climate change is of utmost importance to provide robust scenarios for future biodiversity and to enhance conservation strategies. Recent insights on the factors correlating with declining genetic diversity, population sizes, and local and global extinctions, have been achieved for megafauna species during the Late Quaternary, highlighting the key role of the integration of disciplines like **paleogenomics** and macroecological models [13] to explain range shifts, population collapses, and species extinctions under climate change. More recently, the application of genomics to historical specimens in biological collections is arising as a novel trend to understand genomic erosion of endangered species [75]. Although past biotic turnover and extinction events have provided

better knowledge on extinction dynamics and their relation to climatic changes, paleo-data, together with current data, has only recently been fully implemented in quantitative assessments of future risk of extinction [76]. Moreover, correlative approaches lacking key biological mechanisms have dominated the forecasting of future responses of biodiversity to climate change. A paradigm shift from correlative models of different complexity to process-based simulations informed by paleo-records will bring deeper insights on the interplay of tolerance and dispersal to explain species range dynamics and extinctions under climate change [77] (Box 2 and Figure 2).

Integrating Experimental Approaches, Paleorecords, and Models

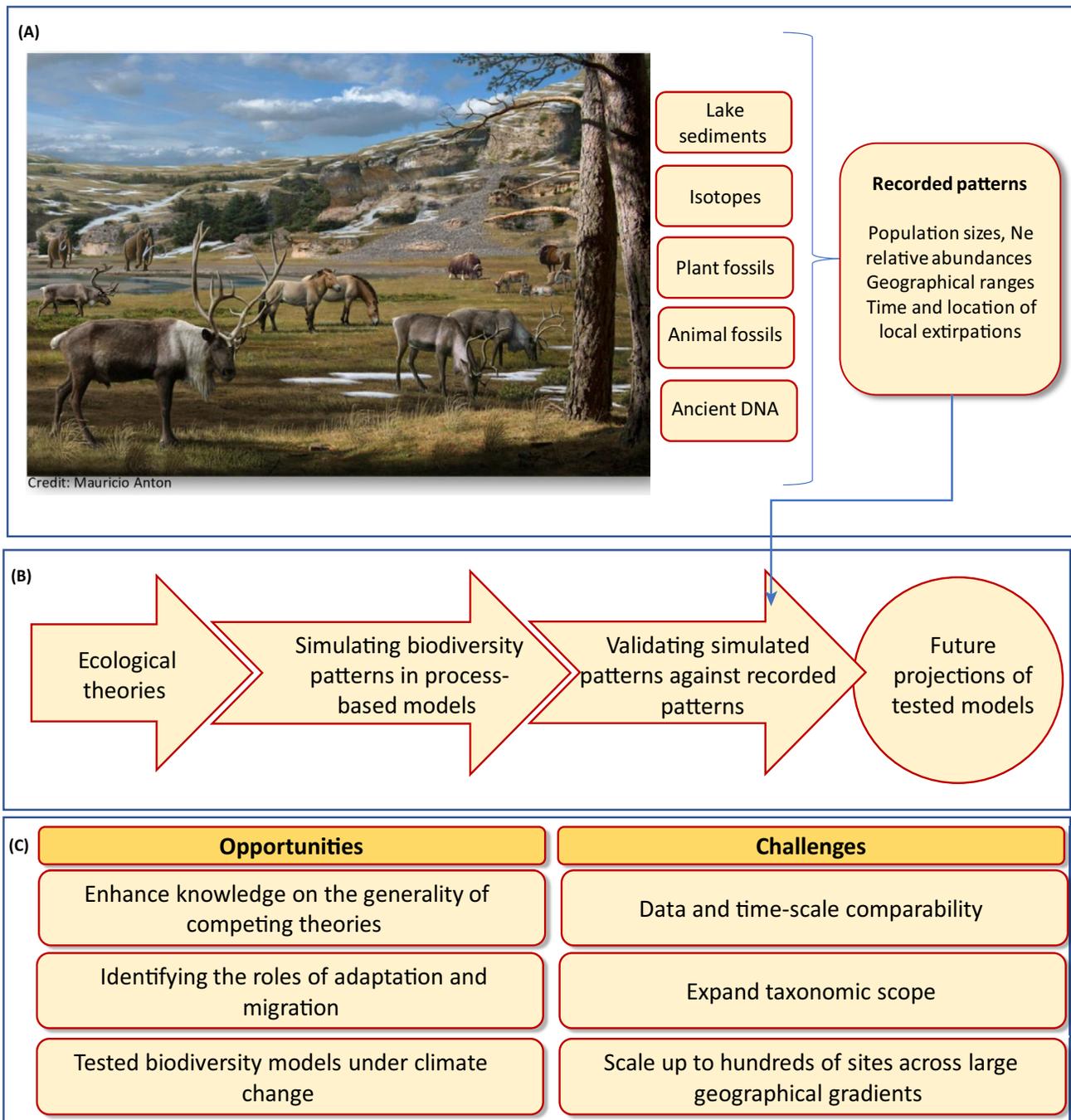
A large gap remains between mechanistic experiments at local- and large-scale macroecological models that forecast the persistence of biological diversity under future global climate change [78]. The integration of **experimental paleoecology**, resurrection ecology, and large-scale **process-based models** holds a great potential to shed light on key mechanisms, as the unveiled role of *in situ* adaptation via evolutionary changes. Their integration can also provide large scale predictions of the magnitude and speed of evolutionary change that species will need to achieve for averting declines and extinction.

Resurrection ecology (RE) focuses on life forms (zooplankton, insects, algae, fungi, bacteria, plants) producing resting stages as part of their life cycles in response to environmental hardship [18,79,80], and its temporal extent encompasses mainly the past 200 years (but see [81]). When such resting stages can be recovered from ancient sediments and reared in the laboratory, they can reveal molecular targets (genes, metabolites, proteins) that enable evolution and adaptation to changing climate. Resurrecting individuals from such species and populations across documented temporal shifts in the environment uniquely permits simultaneous measurement of both plastic (phenotypic and behavioural) and genetic (evolutionary) responses to climatic change, using common garden or transplant experiments [82,83]. Relative fitness of both historical and modern populations can be measured in response to different climatic regimes, including past, present, and future. Such long-term studies, replicated across multiple environments and taxa, can be a powerful resource for building models to forecast species persistence [84] (Figure 1).

A long-standing complement to resurrection ecology might aptly be designated Methuselah ecology (after the biblical character known for his multicentury longevity). Methuselah ecology (ME) focuses on multiple, overlapping generations of living organisms of unusual longevity and

Box 2. Correlations are not Enough: Simulations and Process-Based Models to Improve Biodiversity Forecasts

Much evidence for the impact of past climate change on biodiversity is based on patterns of co-occurrence between past climatic events and biological responses such as migration, tolerance, and extinction. However, the low temporal resolution of available dating techniques for paleorecords often creates difficulties in aligning relevant abiotic dynamics (i. e., climate change, acidification, volcanisms) with biological events. Moving from correlations to causation is challenging because of the co-varying changes in the environment. Recorded biological responses in paleo-records can be used as the testing ground of models deeply rooted in competing ecological and evolutionary theories (see Figure 2 in main text) [103]. In process-based models [104] these records can serve to inform model parameters, test competing hypotheses and scenarios with the paleorecords, and improve predictions. Nonetheless, predictions may be hindered due to limited data availability that stems from low sampling effort, or because the potential for fossilization is not even across regions and species. Given these constraints, vertebrates, and plants from temperate, cold, and dry regions of the planet appear by now as the best suited to apply process-based models in the past. The development and further integration of experiments, paleo-records, and spatial models on past ecosystems will push the envelope of predictive models of biodiversity and the adequacy of theories and different processes to explain past, and future, biodiversity dynamics under climate change.



Trends in Ecology & Evolution

Figure 2. Cracking the Code of Biodiversity Responses to Climate Change. Here we summarize the paleo-data sources, workflow, research challenges, and opportunities to incorporate multiple lines of evidence on the magnitude, rate, and processes involved in biodiversity responses to past climate changes for informing biodiversity scenarios. (A) Digging in the past (here an example of Late Pleistocene in western Europe) to reconstruct, using a variety of paleo-records (i.e., dated fossil records, ancient molecules) and disciplines (paleoecology, population genomics), the past environmental and biotic conditions and responses to past climate change. (B) Main theories and predictions are simulated and tested in process-based models against past recorded trends. (C) Opportunities and challenges ahead to ground future biodiversity scenarios in past biological responses and tested biodiversity models.

studies them to examine demographic, genetic, and ecological responses to environmental change. Tree rings have long been used to reconstruct growth responses to climate variation over centuries to millennia, and also the effects of climate variability on demographic patterns over several centuries [85–87]. In a recent set of studies, tree-ring demography has been combined with genetic studies to examine patterns, rates, and controls of colonization of new sites by *Pinus ponderosa* in western North America, revealing interactions among long-distance dispersal, population genetics, climate variability, and Allee effects [88–90]. Although more difficult to apply to animals, potential exists for simultaneous age and genetic sampling of animals of unusual longevity that can be independently aged (e.g., certain marine fish, tortoises, corals).

Incipient modelling approaches providing spatially explicit predictions of shifts on species distribution and abundance can now incorporate evolutionary adaptation [91]. These models are however in need of quantitative estimates on the magnitude and speed of adaptation, and both resurrection ecology and Methuselah ecology can provide actual values based on historical information. Yet this integration between data and models to forecast future responses at large spatial scales across a variety of taxa faces daunting challenges. Both RE and ME are restricted to a limited set of organisms under a limited set of circumstances (experimental and natural) [80,83]. However, this is not an issue to understanding organismal response to climatic change. Indeed, some species that provide the unique advantage of resurrecting dormant stages are also keystone species in their ecosystem, enabling us to illuminate the links in the causal chain from genes to communities and ecosystems. Ideally, model organisms and systems that feature a comprehensive triad of strong ecological interactions in nature, experimental tractability in diverse contexts, and accessibility to modern genomic tools may be used [92]. The water flea *Daphnia* and the flowering plant *Silene stenophylla*, as well as a number of bacteria, are examples of organisms that satisfy these criteria [15]. They can be used as proxies to study the impact of climatic change on different ecosystems.

Resurrection ecology and Methuselah ecology do not only dig in the past. A forward-in-time approach, involving long-term collection of propagule banks [79,83] will allow scientists in the future to measure the magnitude and speed of evolutionary changes. Under the Project Baseline, seeds of several populations across the geographical range of >60 plant species are now stored and will be grown with contemporaneous seeds during the next 50 years, allowing the identification of phenotypic and molecular evolution occurring during the intervening time under different magnitudes of climate change. Similar initiatives in other continents, and a taxonomic expansion of these experiments, would enable a next generation of predictive models incorporating evolutionary adaptation. Joseph Grinnell in 1910 already foresaw that the most significant value of his field work on Californian fauna would be for the students of the future. Today, his and other pioneers' data have served to document the magnitude and rates of species range shifts and local extirpations in the past century [12,93–96].

Concluding Remarks

Climate change has triggered large and persistent effects on biological diversity, including speciation, redistribution, local adaptations, and extinction events. However, a deeper mechanistic understanding of these dynamics is urgently needed (see Outstanding Questions). Until recently, most evidence suggested that biotic responses to climate change were dominated by range shifting. It is now clear from both paleoecological and ecological perspectives that *in situ* tolerance, being either plasticity or adaptive evolution, are also key responses to climate change. Although adaptation is now an important object of study, we are still lacking sufficient

Outstanding Questions

How far can plasticity enable persistence *in situ*? Most organisms can tolerate changes in the environment by accommodating their morphology, behaviour, and ecophysiology to new environmental conditions. But where is the limit when phenotypic plasticity can no longer sustain real populations under other biotic and abiotic constraints?

Does plasticity evolve under climate change? The evolution of phenotypic plasticity is an important factor for population persistence in a variety of natural systems, but whether selection for increased plasticity is the result of climate change or an emergent trait from selection at shorter scale needs further research. In particular, additional research on the genetic basis and heritability of plasticity is needed so that we can gain a better understanding of conditions under which plasticity is expected to evolve.

How frequent and strong are adaptive responses to climate change?

We still lack more evidences of evolutionary changes driven by climate change. Our ability to detect confidently bottlenecks or adaptive changes embedded in genomic signals in response to climatic or anthropogenic changes depends on the ability to sample before and after a drastic environmental change took place. Long-term monitoring and resurrection ecology approaches can greatly help obtain more information about adaptive responses.

Will species be able to move fast enough?

Dispersal has always been a key response of organisms exposed to changing climates. But given the unprecedented rates and magnitude of ongoing climate change, will species be able to shift ranges at the required pace? In a human-dominated world, what factors determine the variation in effective migration rates?

How well can we predict future extinctions with our current data?

Spatially-explicit mechanistic population models that include traits such as morphology, physiology, phenology, evolutionary adaptive potential, species behaviour, and species

evidence—comparative or experimental—on fundamental questions. How is adaptive evolution shaped by dispersal and range shifting in real ecosystems? Conversely, how is dispersal influenced by adaptive evolution? How do tolerance, adaptive evolution, and dispersal interact in specific circumstances to reduce or amplify risk of extinction? The integration of recorded long-term responses and ecological and evolutionary theories into models will facilitate a deeper understanding of the roles of adaptation and dispersal under climate change. Cracking the code of past biodiversity responses to climate change will increase the ability to anticipate, adapt, and mitigate future declines of biological diversity under climate change.

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interactions are a promising route to improve biodiversity forecasts. These types of models are still in their infancy due to limitations in the available data to calibrate them. More biological and paleobiological data are thus strongly needed, including unrepresented taxa and regions across large climatic and anthropogenic pressure gradients, which highlights the key role of field-work, expeditions, biological collections in natural history museums, herbarium, and museum archives, to resolve the relevant societal challenges of the biodiversity crisis.

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