

2 **Cracking the code of biodiversity responses to past climate**
3 **change**

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25

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

39

40 **Looking to the past to understand the future of biodiversity**

41 Current estimates predict that atmospheric CO₂ levels may rise up to 450-500 ppm by
42 the end of this century, potentially driving an increase in global average temperature on
43 the order of 2 to 5 °C [1]. These projected magnitudes and rates of future climate
44 change, unparalleled in many million years [2], pose major threats to biodiversity [3–6].
45 The scientific community is struggling to fully comprehend the range of responses of
46 biodiversity to climate change, to anticipate whether species can respond quickly
47 enough, and pinpoint the various roles of life-history properties (e.g., dispersal capacity,
48 genetic diversity, reproductive strategies, phenotypic plasticity, population growth rates)
49 in adapting to a changing environment. To make reliable predictions it is essential to
50 advance our understanding of the underlying principles and mechanisms of biodiversity

51 responses. One fruitful approach is to look to the past by using geo-historical records to
52 learn how individuals, populations, communities and biomes have responded to
53 previous climatic changes [7–11]. Whether individuals and populations will adapt by
54 evolutionary change or plasticity, whether they will migrate fast enough, and whether
55 those responses will be adequate to forestall collapses of species ranges and prevent
56 widespread species extinctions can be explored using case studies from the past.
57 Indeed, past climate change, whether abrupt or gradual, and whether occurring in deep
58 time or recent history, offers a vast set of unplanned natural experiments to explore
59 biodiversity responses and test ecological and evolutionary theories. Recent years have
60 seen the accumulation of well-documented examples of the influence of climate change
61 on persistence, adaptation and diversification, dispersal, and extinction (e.g. [12–15]).
62 The effects of climate change on rates and routes of range shifts have been intensively
63 studied by biogeographers and paleoecologists, augmented recently by molecular
64 markers and ancient DNA (aDNA; [16,17]). *In situ* tolerance to changing climate
65 conditions has been explored in the fossil record using functional morphology and
66 evolutionary genetics, including recent experimental approaches like ‘resurrection
67 ecology [15,18,19]. Finally, paleoecological records of local and global extinctions
68 provide information on the nature and consequences of failure of *in situ* tolerance and
69 range shifts [20,21].
70
71 However, key knowledge gaps remain. The relative importance of different mechanisms
72 involved in species tolerance (e.g., evolutionary adaptive change versus phenotypic
73 plasticity), and the nature and rates of climate-driven anagenetic evolution - a transition
74 of one species to another- and cladogenetic evolution - the separation of a species into
75 two or more species or clades- remain poorly understood [22]. The relative efficacy of

76 *in situ* tolerance and range shifting under different rates and magnitudes of climate
77 change is obscure [23,24]. Although much attention has been devoted to
78 paleoecological records of species' range shifts [25], the speed and underlying controls
79 are not clear except in a few specific cases [24]. Moreover, significant challenges
80 remain for better integrating knowledge, scales, methods and data from a variety of
81 biological disciplines, from paleoecology to genomics. In this review, we (1) synthesize
82 the main responses of biodiversity to past climate change from deep to recent time
83 (tolerance *in situ*, range shifts, and their simultaneous failure, resulting in extinction),
84 (2) identify key knowledge gaps concerning underlying mechanisms (which span a
85 broad set of biological disciplines), and (3) review and discuss new approaches that
86 integrate multiple methods and disciplines to better understand the strategies by which
87 life adapts to climate change and to better anticipate future responses of biological
88 diversity.

89

90 **Biodiversity responses to climate change**

91 Tolerance, Adaptive Evolution, and Diversification

92 Biotic responses to climatic and environmental changes as shown by the fossil records
93 vary from macroevolutionary divergences (at very long (10^6 - 10^7 yr) time scales), to
94 adaptive evolution (10^0 - 10^5 yr), to phenotypic adjustments in place (10^{-1} - 10^3 yr). Long-
95 term climate change has been considered an important driver of high-order
96 diversification, as clades respond to new climatic regimes [14]. In shorter time spans,
97 many individuals and populations (e.g. long-lived modular organisms like corals and
98 plant genets) can tolerate a high degree of climate change *in situ*. Paleogenetic records
99 suggest also that adaptive evolution can support long-term persistence of species in

100 response to climate change [26]. Adaptations can enable exploitation of new niches: for
101 example, adaptive mutations in woolly mammoth haemoglobin allowed the exploitation
102 of high-latitude cold environments during the Pleistocene [27]. Examples of more
103 recent microevolutionary responses to climatic change include changes in the body
104 color of owls during warmer winters [28], or adaptive changes in the flowering time of
105 Brassicas in response to drought [29].

106

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

116 Range shifts

117 Range shifting (usually referred as migration in paleo-disciplines) has been a dominant
118 response of species to climate shifts in the past [25]. Past range shifts are typically
119 inferred from spatial and temporal patterns in fossil data [36,37], geographic patterns in
120 genetic markers of extant and extinct populations [17], or both (e.g. [38]). They have
121 shown variable species-specific spatial trajectories, timing and migration rates, ranging
122 from a few tens to a few thousand m/yr, with averages around 2.7 km/decade [39–41].
123 Overall, there is evidence of both rapid range shifts and community reshuffling [42] as

124 well as many species lagging behind climate [43], which reinforces the high specificity
125 of range shift patterns across taxa.

126

127 There are many different mechanisms by which climate change influences range shifts
128 [44]. First, climate change can improve suitability beyond the range limit so that species
129 may establish at formerly unsuitable areas like higher latitudes or altitudes [45,46]. .

130 Second, climate change could foster colonisation of new areas in several ways:
131 enhanced fecundity of source populations (thus increasing propagule pressure),
132 increased propensity to disperse or emigrate (particularly in animals), or acceleration of
133 dispersal processes [47,48]. Climate change can also enhance establishment of
134 propagules after arrival, both directly [49] and –particularly in rapid climate change– by
135 reducing populations of dominant species, via mortality or disturbance [50]. Finally,
136 climate change could reduce the probability of extinction of leading edge populations,
137 for instance due to extreme climatic events [51]. A variety of processes are involved in
138 species’ range shifts, all of which can be directly or indirectly (e.g. mediated by species
139 interactions) influenced by climate change [23,50,52,53]. A challenge for ecologists,
140 biogeographers, and paleoecologists is to identify generalizations, and to understand the
141 role of species-specific, locale-specific, and time-specific contingencies and
142 idiosyncracies in driving patterns and rates of range shifts.

143

144 Extinction

145 When species cannot tolerate climate change *in situ*, or colonize suitable habitat
146 elsewhere quickly enough, they become extinct. In extreme cases, many high-order
147 clades can be lost in mass extinction events [54,55]. There is strong support for a
148 primary role of climate change, alone or in connection to other factors, in extinction

149 events of different magnitude over the last 500 million years, including the recent
150 extinction of large mammals in the last 50,000 years [21]. Evidence of climate-driven
151 species extinctions in recent centuries is limited [56], with rare exceptions being
152 synergistic functions of both 20th century human-induced climate change and other
153 proximate drivers of extinction (including infectious diseases) [57]. However,
154 anthropogenic climate disruption is predicted to soon compete with habitat destruction
155 as the most important driver of contemporary extinctions [58,59].

156

157 Climate change may trigger extinctions and local extirpations by surpassing the
158 physiological limits of species, by reducing primary productivity of ecosystems and
159 thereby local population fitness across food webs, and indirectly by disrupting
160 ecological interactions via changes in species distributions or phenology. For instance,
161 coral bleaching, the loss of intracellular endosymbionts due to the increase in
162 prevalence of extreme heating episodes and changes in the carbon cycle, is one of the
163 main supported mechanisms behind coral extinctions during the five mass extinction
164 events [60]. Also, drier and colder climatic conditions during the LGM triggered a
165 reduction in overall primary productivity, provoking losses in genetic diversity and
166 populations of large grazers [13], depleting lineages, for example, of bowhead whales
167 [61], and contributing to local and global extinctions [21]. These pathways to
168 extinctions in different periods of the Earth's history share some commonalities. In
169 particular, climatic changes that exceed in magnitude and speed those experienced
170 during the evolutionary history of species usually trigger extinction events, and climate
171 change has frequently interacted with other extinction drivers [61].

172 **Unknowns, challenges and routes ahead**

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

177

178 Evolutionary adaptation versus plasticity?

179

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

187 At deep-time scales, comparative phylogenetics and novel macroevolutionary
188 approaches are offering new insights into speciation and phenotypic change in response
189 to major climatic shifts [63]. For instance, it was found that expected future climate
190 change largely surpass past rates of climatic niche evolution among vertebrate species
191 [64]. Comparative approaches allow fitting various models of phenotypic evolution and
192 diversification to phylogenies in order to estimate evolutionary rates, including
193 speciation and extinction [14]. Recently, models that can explicitly test for the effect of
194 climatic changes on these evolutionary rates have been developed [65–68]. Future
195 studies including genomic level data across thousands of species and climate-dependent

196 evolutionary models will provide deeper insights on the role of climate change on
197 speciation, including bursts, and phenotypic change.

198

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

213

214 Migrating fast enough?

215

216 Although dispersal is a key process underlying range shifts and the spread of native and
217 invasive species, the migration capacity of species under rapid climate change remains
218 uncertain [23]. While some taxa seem unable to shift ranges under changing climates
219 [43], others seem able to migrate at a fast pace [45]. Attempts to explain observed range
220 shifts based on species traits or ecological strategies have obtained modest results

221 [71,72] (but see [73]). Low predictability may be expected given the large number of
222 processes involved in range shifts, as well as the complexity and path-dependence when
223 those processes interact. The dispersal process itself is highly stochastic and inherently
224 uncertain [74]. Other important processes include size and fecundity of source
225 populations (which determine propagule pressure), gene flow, local adaptation,
226 evolution of dispersal, biotic interactions (competition, facilitation, mutualisms), Allee
227 effects, and so on, all of which are likely to be affected by climate change [23]. Spatial
228 heterogeneity on the landscape plays a role (e.g., dispersal-target size), as does high-
229 frequency climate variability [47,50]. As a result, we may not be able to go much farther
230 than estimating dispersal potentials for different species or populations [74]. A critical
231 challenge is to use paleoecological and ecological data to identify generalizations that
232 can emerge from the location-specific, species-specific, and event-specific particulars of
233 detailed case studies [47,50].

234

235 Paleoecology has largely contributed to estimate how fast species migrated under past
236 climatic changes under minimum levels of pre-historic global human intervention.
237 Unfortunately, contemporaneous dispersal rates are likely to be rather different than past
238 rates due to radically different conditions: more fragmented habitats, missing and novel
239 interactions, or nearly unlimited human-mediated dispersal [23]. Hence, estimates of
240 past migrations rates, however informative, may be of limited value when attempting to
241 forecast future range shifts. Instead, a better understanding of the causes of variation in
242 range shift rates may move us forward. Comparative studies of range shifts patterns
243 among tens or even hundreds of species could throw some light into the role of
244 environmental (contingent) factors as well as intrinsic factors that make some species
245 migrate faster, slower or not at all.

246

247 Anticipating future extinctions

248 Revealing how the accumulative failure of *in situ* tolerance and dispersal mechanisms
249 leads to population extirpation and ultimately species extinction under climate change is
250 of utmost importance to provide robust scenarios for future biodiversity and to enhance
251 conservation strategies. Recent insights on the factors correlating with declining genetic
252 diversity, population sizes, and local and global extinctions, have been achieved for
253 megafauna species during the Late Quaternary, highlighting the key role of the
254 integration of disciplines like paleo-genomics and macroecological models [13] to
255 explain range shifts, population collapses and species extinctions under climate change.
256 More recently the application of genomics to historical specimens in biological
257 collections is arising as a novel trend to understand genomic erosion of endangered
258 species [75]. Although past biotic turnover and extinction events have provided better
259 knowledge on extinction dynamics and their relation to climatic changes, paleo-data
260 together with current data has only recently been fully implemented in quantitative
261 assessments of future risk of extinction [76]. Moreover, correlative approaches lacking
262 key biological mechanisms have dominated the forecasting of future responses of
263 biodiversity to climate change. A paradigm shift from correlative models of different
264 complexity to process-based simulations informed by paleo-records will bring deeper
265 insights on the interplay of tolerance and dispersal to explain species range dynamics
266 and extinctions under climate change [77] (Box 2; Figure 2).

267

268 Integrating experimental approaches, paleorecords and models

269 A large gap remains between mechanistic experiments at local scales and large-scale
270 macroecological models that forecast the persistence of biological diversity under future

271 global climate change [78]. The integration of experimental paleoecology, resurrection
272 ecology, and large-scale process-based models holds a great potential to shed light on
273 key mechanisms, as the unveiled role of in situ adaptation via evolutionary changes.
274 Their integration can also provide large scales predictions of the magnitude and speed
275 of evolutionary change that species will need to achieve for averting declines and
276 extinction.

277

278 Resurrection Ecology (RE) focuses on life forms (zooplankton, insects, algae, fungi,
279 bacteria, plants) producing resting stages as part of their life cycles in response to
280 environmental hardship [18,79,80], and its temporal extent encompasses mainly the last
281 200 years (but see [81]). When such resting stages can be recovered from ancient
282 sediments and reared in the laboratory, they can reveal molecular targets (genes,
283 metabolites, proteins) that enable evolution and adaptation to changing climate.
284 Resurrecting individuals from such species and populations across documented
285 temporal shifts in the environment uniquely permits simultaneous measurement of both
286 plastic (phenotypic and behavioural) and genetic (evolutionary) responses to climatic
287 change, using common garden or transplant experiments [82,83]. Relative fitness of
288 both historical and modern populations can be measured in response to different
289 climatic regimes, including past, present and future. Such long-term studies, replicated
290 across multiple environments and taxa, can be a powerful resource for building models
291 to forecast species persistence [84] (Figure 1).

292

293 A long-standing complement to resurrection ecology might aptly be designated
294 Methuselan ecology (after the biblical character known for his multi-century longevity).
295 Methuselan ecology (ME) focuses on multiple, overlapping generations of living

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

307

308 Incipient modelling approaches providing spatially explicit predictions of shifts on
309 species distribution and abundance can now incorporate evolutionary adaptation [91].
310 These models are however in need of quantitative estimates on the magnitude and speed
311 of adaptation, and both Resurrection Ecology and Methuselan ecology can provide
312 actual values based on historical information. Yet this integration between data and
313 models to forecast future responses at large spatial scales across a variety of taxa faces
314 daunting challenges. Both RE and ME are restricted to a limited set of organisms under
315 a limited set of circumstances (experimental and natural) [80,83]. However, this is not
316 an issue to understanding organismal response to climatic change. Indeed, some species
317 that provide the unique advantage of resurrecting dormant stages are also keystone
318 species in their ecosystem, enabling us to illuminate the links in the causal chain from
319 genes to communities and ecosystems. Ideally, model organisms and systems that
320 feature a comprehensive triad of strong ecological interactions in nature, experimental

321 tractability in diverse contexts and accessibility to modern genomic tools, may be used
322 [92]. The water flea *Daphnia* and the flowering plant *Silene stenophylla*, as well as a
323 number of bacteria are examples of organisms that satisfy these criteria [15]. They can
324 be used as proxies to study the impact of climatic change on different ecosystems.

325

326 Resurrection Ecology and Methuselan ecology do not only dig in the past. A forward-
327 in-time approach, involving long-term collection of propagule-banks [79,83] will
328 allow scientists in the future to measure the magnitude and speed of evolutionary
329 changes. Under the Project Baseline, seeds of several populations across the
330 geographical range of >60 plant species are now stored and will be grown with
331 contemporaneous seeds during the next 50 years, allowing the identification of
332 phenotypic and molecular evolution occurring during the intervening time under
333 different magnitudes of climate change. Similar initiatives in other continents, and a
334 taxonomic expansion of these experiments, would enable a next generation of predictive
335 models incorporating evolutionary adaptation. Joseph Grinnell in 1910 already foresaw
336 that the most significant value of his field work on Californian fauna would be for the
337 students of the future. Today, his and other pioneers' data have served to document the
338 magnitude and rates of species range shifts and local extirpations in the last century
339 [12,93–96].

340

341 **Concluding remarks**

342 Climate change has triggered large and persistent effects on biological diversity,
343 including speciation, redistribution, local adaptations and extinction events. However, a
344 deeper mechanistic understanding of these dynamics is urgently needed (see also
345 Outstanding Questions). Until recently, most evidence suggested that biotic responses to

346 climate change were dominated by range shifting. It is now clear from both
347 paleoecological and ecological perspectives that *in situ* tolerance, being plasticity or
348 adaptive evolution, are also key responses to climate change. Although adaptation is
349 now an important object of study, we are still lacking sufficient evidence - comparative
350 or experimental - on fundamental questions: How is adaptive evolution shaped by
351 dispersal and range shifting in real ecosystems? Conversely, how is dispersal influenced
352 by adaptive evolution? How do tolerance, adaptive evolution, and dispersal interact in
353 specific circumstances to reduce or amplify risk of extinction? The integration of
354 recorded long-term responses and ecological and evolutionary theories into models will
355 facilitate a deeper understanding of the roles of adaptation and dispersal under climate
356 change. Cracking the code of past biodiversity responses to climate change will increase
357 the ability to anticipate, adapt and mitigate future declines of biological diversity under
358 climate change.

359

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624

625 **Glossary**

626 **Adaptive evolution** –Results from the propagation of advantageous alleles in populations
627 through natural selection, driven by environmental selection pressure acting on genes
628 underlying species traits linked to fitness.

629 **Dormant propagules** – A still living seed, cyst, spore or egg that has arrested development and
630 is preserved in ice, soil, sediment, permafrost.

631 **Experimental Paleocology:** Experimental studies to test sufficiency and necessity of
632 mechanisms (or combinations or sequences of mechanisms) invoked to explain paleoecological
633 phenomena.

634 **Migration** – Spatial displacement of organisms leading to shifts of species distributions

635 **Paleogenomics** – The study of ancient genomes to reveal functional genetic patterns through
636 time, supporting inferences concerning evolutionary adaptation, functional traits, population
637 dynamics, domestication, genetic events preceding extirpations or extinctions, and other
638 patterns of interest.

639 **Phenotypic plasticity** – Ability of individuals of a genotype to alter physiology, morphology,
640 anatomy, phenology, behaviour, or other phenotypic traits in response to environmental change.

641 **Resurrection ecology** – Study of traits and environmental responses of past populations by
642 hatching or germination of dormant propagules and culturing or cultivation of the organisms.

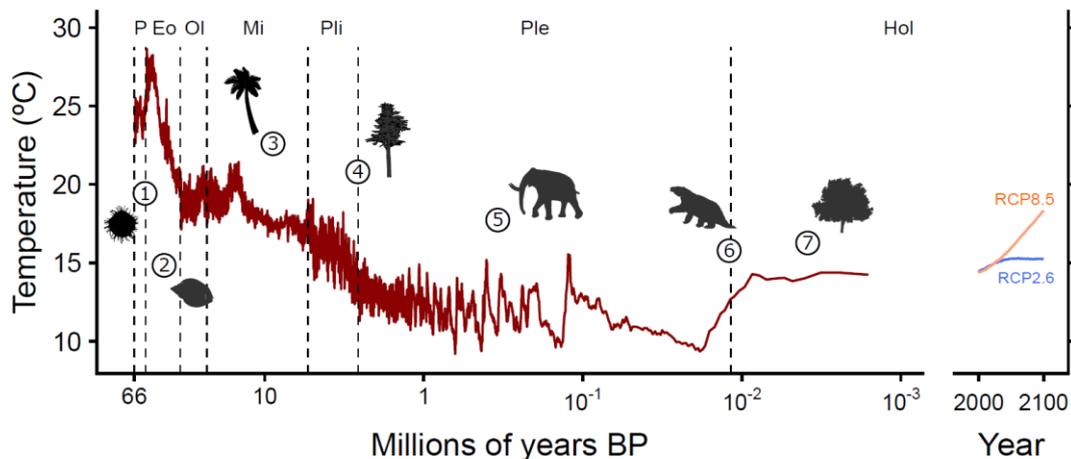
643 **Process-based models** - Spatially explicit approaches that simulate the effect of climate and
644 environmental conditions on important vital rates (including population growth, dispersal and
645 plasticity in demographic traits) to explain species distributions and their changes, including
646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

647 **Tolerance** –Ability of a population to persist at a site under environmental change by adaptive
648 evolution, phenotypic plasticity, or both.

649

650

651 **Box 1. Biodiversity responses to past climate change.**



652

653 **Figure I:** Future climate forcing will surpass those of the previous several million years [2].

654 Countless individuals in thousands of species across the globe will need to tolerate climate
 655 change *in situ*, disperse to more suitable climatic conditions, or undergo extinction. Figure I

656 highlights a number of biodiversity responses directly or indirectly linked to climatic changes
 657 along the Cenozoic (last 66 million years). 1) During the Paleocene-Eocene Thermal Maximum

658 (~56 million years before present) there were large extinctions in some marine groups (benthic
 659 foraminifera), remarkable poleward range shifts in others (dinoflagellates, mammals, reptiles,

660 plants), and high community turnover [97]. 2) Under a global cooling trend, winters became
 661 >4 °C colder across the Eocene-Oligocene boundary, partially driving extinction of many

662 terrestrial mammals in Europe as well as marine invertebrates globally [98]. 3) Many
 663 thermophilous plants shifted their ranges southward and finally went extinct in Europe during

664 the late Miocene global cooling [99]. 4) More than half (52%) of the cool-temperate European
 665 tree genera did not survive the glaciation cycles starting at the end of the Pliocene [100]. 5) An

666 adaptive mutation of haemoglobin enabled mammoths to tolerate the very low temperatures at
 667 high latitudes [27]. 6) More than 70% of megafauna genera in the Americas and Australia, and

668 40% in Eurasia, underwent extinction within a relatively brief period of time (5,000-10,000
 669 years) in co-occurrence with climatic changes and human impacts [55]. 7) Plants in North

670 America migrated northwards between 450 and 2200 km in less than 10,000 years under a
 671 warming of 5 degrees [101]. Past temperature data from [102]; future temperature projections

672 (under two greenhouse concentration scenarios: RCP2.5, most benign, and RCP8.6, most
673 extreme) from [1]. Abbreviations of geological epochs as follows: P = Palaeocene, Eo =
674 Eocene, Ol = Oligocene, Mi = Miocene, Pli = Pliocene, Ple = Pleistocene, Hol = Holocene.

675

676

677 **Box 2. Correlations are not enough: simulations and process-based models to**
678 **improve biodiversity forecasts**

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

698

699 **Box 3. Outstanding Questions**

700

701 **- How far can plasticity enable persistence *in situ*?** Most organisms can tolerate changes in
702 the environment by accommodating their morphology, behavior, ecophysiology, to new

703 environmental conditions. But where is the limit when phenotypic plasticity can no longer
704 sustain real populations under other biotic and abiotic constraints?

705

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

712

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

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

723

724 **-How well can we predict future extinctions with our current data?** Spatially-explicit
725 mechanistic population models that include traits such as morphology, physiology, phenology,
726 evolutionary adaptive potential, species behavior and species interactions are a promising route
727 to improve biodiversity forecasts. These types of models are still in their infancy due to
728 limitations in the available data to calibrate them. More biological and paleobiological data are
729 thus strongly needed, including unrepresented taxa and regions across large climatic and
730 anthropogenic pressure gradients, which highlights the key role of field-work, expeditions,

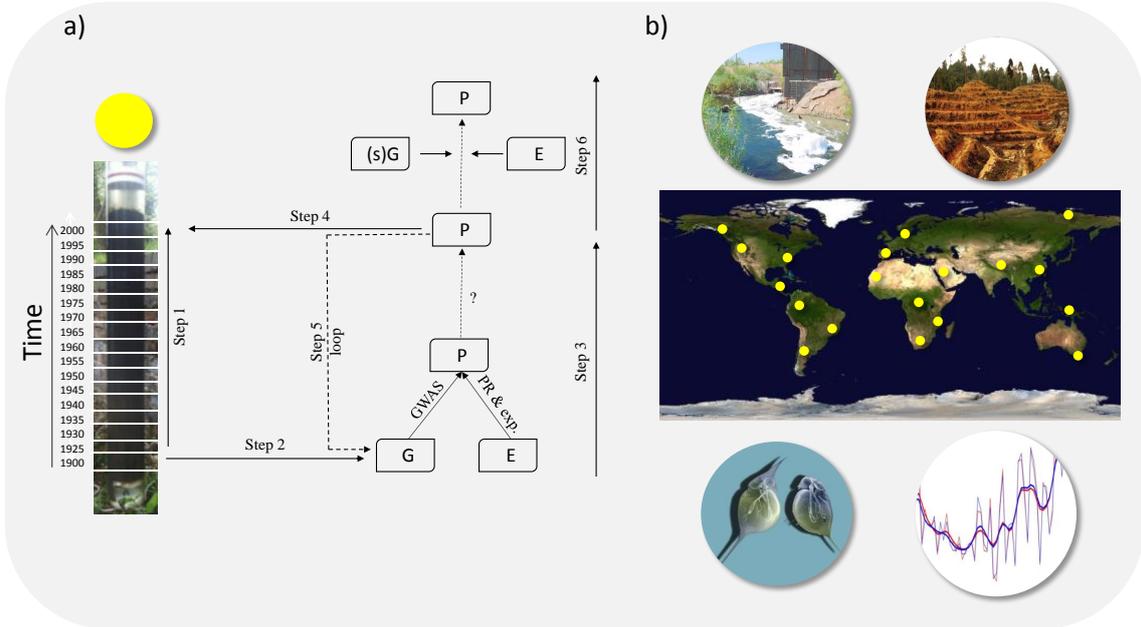
731 biological collections in natural history museums, herbarium and museum archives, to resolve
732 the relevant societal challenges of the biodiversity crisis.

733

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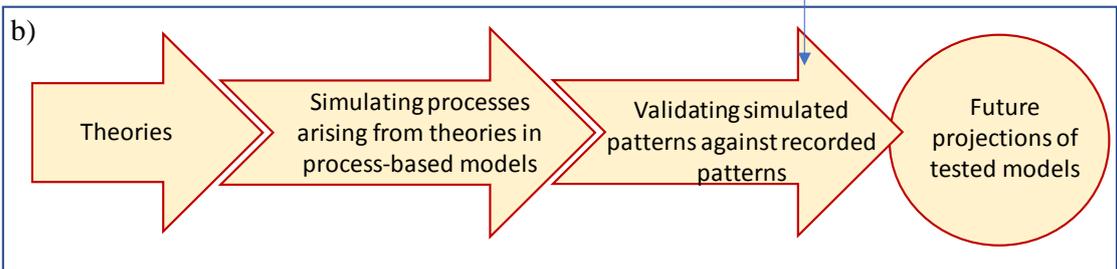
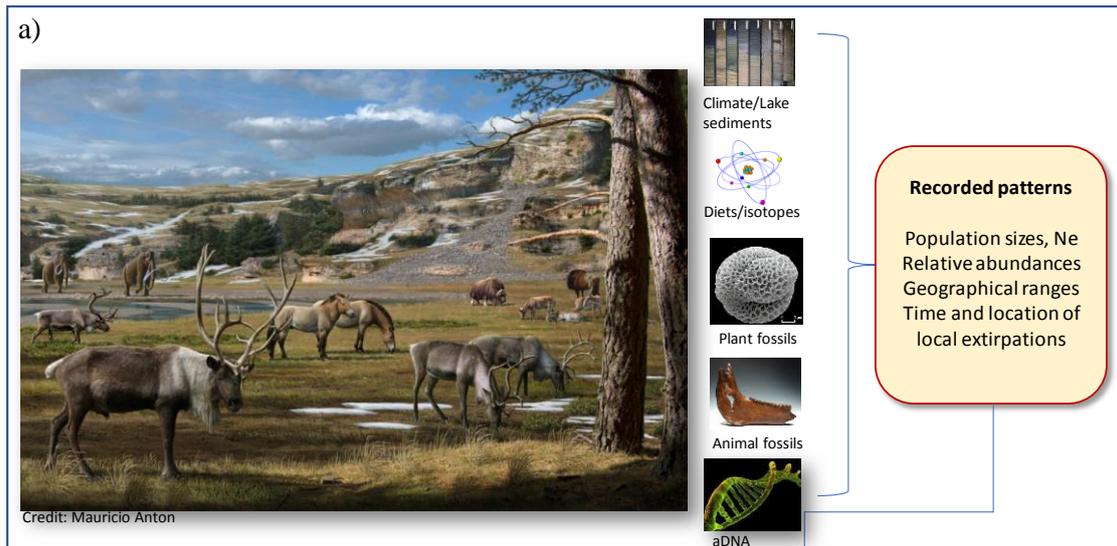
736 **Figure 1. Reconstructing historical patterns of evolutionary change for unravelling**
737 **mechanisms of genetic and plastic response to anthropogenic environmental**
738 **changes. a)** Conceptual framework for the integration of resurrection ecology and
739 predictive models. Using for example *Daphnia*, dormant propagules can be resurrected
740 (step 1). On resurrected propagules, genetic (G) and phenotypic changes (P) can be
741 quantified over evolutionary time. Similarly, environmental factors (E) can be inferred
742 from historical records or measured e.g. via chemical analysis of sediment. The genetic
743 mechanisms (G) underlying phenotypic changes (P) are identified via a genome wide
744 association analysis (GWAS) (step 2). The causal link between phenotypic changes (P)
745 and environmental variation (E) is established via experiments with the support of
746 historical environmental records or reconstruction of temporal trends in environmental
747 variables (PR). The parameters for predictive models of phenotypic trajectories are
748 trained on empirical data (G, P and E) from the sedimentary archive (step 5). Several
749 iterations may be needed to identify the parameters that best fit the empirical data.
750 Using the optimized parameters, future trajectories of phenotypic (and the underlying
751 genotypic) trajectories are identified, with a level of uncertainty (step 6). **b)** Scaling up
752 the approach described in a) to a macroecological scale, across sites -represented by
753 yellow circle- and biological systems within ecosystems from the tropics to the poles,
754 we can identify evolutionary and plastic responses of species to global anthropogenic
755 pressures (within circles from upper left to bottom right: habitat degradation, land-use
756 changes, invasive species and climate change).



757

758

759 **Figure 2 Cracking the code of biodiversity responses to climate change.** Here we
760 summarize the paleo-data sources, workflow, research challenges and opportunities to
761 incorporate multiple lines of evidence on the magnitude, rate, and processes involved on
762 biodiversity responses to past climate changes for informing biodiversity scenarios. a)
763 Digging in the past (here an example of Late Pleistocene in western Europe) to
764 reconstruct, using a variety of paleo-records (i.e., dated fossil records, ancient
765 molecules) and disciplines (paleoecology, population genomics), the past environmental
766 and biotic conditions and responses to past climate change. b) Main theories and
767 predictions are simulated and tested in process-based models against past recorded
768 trends. c) Opportunities and challenges ahead to ground future biodiversity scenarios in
769 past biological responses and tested biodiversity models.
770



c)

Opportunities	Challenges
Enhance knowledge on the generality of competing theories	Data and time-scale comparability
Identifying the roles of adaptation and migration	Expand taxonomic scope
Tested biodiversity models under climate change	Scale up to hundreds of sites across large geographical gradients