

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

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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 CO<sub>2</sub> 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 20<sup>th</sup> 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 CO<sub>2</sub>  
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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369

### 370 **References**

371

- 372 1 IPCC (2013) *Climate Change 2013 - The Physical Science Basis: Working*  
373 *Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on*  
374 *Climate Change*, Cambridge University Press.
- 375 2 Foster, G.L. *et al.* (2017) Future climate forcing potentially without precedent in  
376 the last 420 million years. *Nature Communications* 8, 14845
- 377 3 Moritz, C. and Agudo, R. (2013) The Future of Species Under Climate Change:  
378 Resilience or Decline? *Science* 341, 504–508
- 379 4 Urban, M.C. (2015) Accelerating extinction risk from climate change. *Science*  
380 348, 571–573
- 381 5 Pecl, G. (2017) Biodiversity redistribution under climate change: Impacts on  
382 ecosystems and human well-being. *Science* 355, 6332
- 383 6 Garcia, R.A. *et al.* (2014) Multiple Dimensions of Climate Change and Their  
384 Implications for Biodiversity. *Science* 344, 1247579
- 385 7 Jackson, S.T. and Overpeck, J.T. (2000) Responses of plant populations and  
386 communities to environmental changes of the late Quaternary. *Paleobiology* 26, 194–  
387 220
- 388 8 Willis, K.J. *et al.* (2010) Biodiversity baselines, thresholds and resilience: testing  
389 predictions and assumptions using palaeoecological data. *Trends in Ecology &*  
390 *Evolution* 25, 583–591
- 391 9 Dawson, T.P. *et al.* (2011) Beyond Predictions: Biodiversity Conservation in a  
392 Changing Climate. *Science* 332, 53–58
- 393 10 Fritz, S.A. *et al.* (2013) Diversity in time and space: wanted dead and alive.  
394 *Trends in Ecology & Evolution* 28, 509–516
- 395 11 Barnosky, A.D. *et al.* (2017) Merging paleobiology with conservation biology to



396 guide the future of terrestrial ecosystems. *Science* 355, eaah4787

397 12 Moritz, C. *et al.* (2008) Impact of a Century of Climate Change on Small-

398 Mammal Communities in Yosemite National Park, USA. *Science* 322, 261–264

399 13 Lorenzen, E.D. (2011) Species-specific responses of Late Quaternary megafauna

400 to climate and humans. *Nature* 479, 359–364

401 14 Condamine, F.L. *et al.* (2013) Macroevolutionary perspectives to environmental

402 change. *Ecology Letters* 16, 72–85

403 15 Orsini, L. *et al.* (2013) The evolutionary time machine: using dormant

404 propagules to forecast how populations can adapt to changing environments. *Trends in*

405 *Ecology & Evolution* 28, 274–282

406 16 Der Sarkissian, C. *et al.* (2014) Ancient genomics. *Philosophical Transactions*

407 *of the Royal Society B: Biological Sciences* 370, 20130387–20130387

408 17 Hewitt, G.M. (2004) Genetic consequences of climatic oscillations in the

409 Quaternary. *Philosophical Transactions of the Royal Society B: Biological Sciences*

410 359, 183–195

411 18 Kerfoot, W.C. and Weider, L.J. (2004) Experimental paleoecology (resurrection

412 ecology): Chasing Van Valen’s Red Queen hypothesis. *Limnology and Oceanography*

413 49, 1300–1316

414 19 Orsini, L. *et al.* (2016) Temporal genetic stability in natural populations of the

415 waterflea *Daphnia magna* in response to strong selection pressure. *Molecular Ecology*

416 25, 6024–6038

417 20 Jackson, S.T. and Weng, C. (1999) Late Quaternary extinction of a tree species

418 in eastern North America. *Proceedings of the National Academy of Sciences* 96, 13847–

419 13852

420 21 Cooper, A. *et al.* (2015) Abrupt warming events drove Late Pleistocene

421 Holarctic megafaunal turnover. *Science* 349, 602–606

422 22 Merila, J. and Hendry, A.P. (2014) Climate change, adaptation, and phenotypic  
423 plasticity: the problem and the evidence. *Evolutionary Applications* 7, 1–14

424 23 Corlett, R.T. and Westcott, D.A. (2013) Will plant movements keep up with  
425 climate change? *Trends in Ecology & Evolution* 28, 482–488

426 24 Pearson, R. (2006) Climate change and the migration capacity of species. *Trends*  
427 *Ecol. Evol* 21, 111–113

428 25 Huntley, B. and Webb, T. (1989) Migration: species' response to climatic  
429 variations caused by changes in the earth's orbit. *J. Biogeogr* 16, 5–19

430 26 Davis, M.B. *et al.* (2005) Evolutionary responses to changing climate. *Ecology*  
431 86, 1704–1714

432 27 Campbell, K.L. *et al.* (2010) Substitutions in woolly mammoth hemoglobin  
433 confer biochemical properties adaptive for cold tolerance. *Nature Genetics* 42, 536–540

434 28 Karrel, P. (2011) Climate change drives microevolution in a wild bird. *Nature*  
435 *Communications* 2, 208

436 29 Franks, S.J. *et al.* (2007) Rapid evolution of flowering time by an annual plant in  
437 response to a climate fluctuation. *Proceedings of the National Academy of Sciences* 104,  
438 1278–1282

439 30 Richardson, J.L. *et al.* (2014) Microgeographic adaptation and the spatial scale  
440 of evolution. *Trends in Ecology & Evolution* 29, 165–176

441 31 Hendry, A.P. *et al.* (2008) Human influences on rates of phenotypic change in  
442 wild animal populations. *Molecular Ecology* 17, 20–29

443 32 Charmantier, A. *et al.* (2008) Adaptive Phenotypic Plasticity in Response to  
444 Climate Change in a Wild Bird Population. *Science* 320, 800–803

445 33 Charmantier, A. and Gienapp, P. (2014) Climate change and timing of avian

446 breeding and migration: evolutionary versus plastic changes. *Evol. Appl* 7, 15–28

447 34 Franks, S.J. *et al.* (2013) Evolutionary and plastic responses to climate change in  
448 terrestrial plant populations. *Evolutionary Applications* 7, 123–139

449 35 Reusch, T.B.H. (2013) Climate change in the oceans: evolutionary versus  
450 phenotypically plastic responses of marine animals and plants. *Evolutionary*  
451 *Applications* 7, 104–122

452 36 Huntley, B. and Birks, H.J.B. (1983) An atlas of past and present pollen maps  
453 for Europe, 0-13,000 years ago. Cambridge University Press

454 37 Jackson, S.T. *et al.* (1997) Mapped plant-macrofossil and pollen records of late  
455 Quaternary vegetation change in Eastern North America. *Quaternary Science Reviews*  
456 16, 1–70

457 38 Norris, J.R. *et al.* (2015) Late Holocene expansion of ponderosa pine (*Pinus*  
458 *ponderosa*) in the Central Rocky Mountains, USA. *Journal of Biogeography* 43, 778–  
459 790

460 39 Blois, J.L. (2013) Narrowing the estimates of species migration rates. *Frontiers*  
461 *Biogeogr* 5, 19448

462 40 Feurdean, A. *et al.* (2013) Tree migration-rates: narrowing the gap between  
463 inferred post-glacial rates and projected rates. *PLoS ONE* 8, 71797

464 41 Ordóñez, A. and Williams, J.W. (2013) Climatic and biotic velocities for woody  
465 taxa distributions over the last 16 000 years in eastern North America. *Ecology Letters*  
466 16, 773–781

467 42 Tinner, W. and Lotter, A.F. (2001) Central European vegetation response to  
468 abrupt climate change at 8.2 ka. *Geology* 29, 551

469 43 Normand, S. *et al.* (2011) Postglacial migration supplements climate in  
470 determining plant species ranges in Europe. *Proceedings of the Royal Society B:*

471 *Biological Sciences* 278, 3644–3653

472 44 Holt, R.D. and Keitt, T.H. (2000) Alternative causes for range limits: a  
473 metapopulation perspective. *Ecology Letters* 3, 41–47

474 45 Chen, I.-C. *et al.* (2011) Rapid Range Shifts of Species Associated with High  
475 Levels of Climate Warming. *Science* 333, 1024–1026

476 46 Hodgson, J.A. *et al.* (2015) Predicting microscale shifts in the distribution of the  
477 butterfly *Plebejus argus* at the northern edge of its range. *Ecography* 38, 998–1005

478 47 Lyford, M.E. *et al.* (2003) Influence of landscape structure and climate  
479 variability on a late Holocene plant migration. *Ecological Monographs* 73, 567–583

480 48 Battisti, A. (2006) A rapid altitudinal range expansion in the pine processionary  
481 moth produced by the 2003 climatic anomaly. *Glob. Change Biol* 12, 662–671

482 49 Wethey, D.S. *et al.* (2011) Response of intertidal populations to climate: Effects  
483 of extreme events versus long term change. *Journal of Experimental Marine Biology*  
484 *and Ecology* 400, 132–144

485 50 Jackson, S.T. *et al.* (2009) Ecology and the ratchet of events: Climate variability,  
486 niche dimensions, and species distributions. *Proceedings of the National Academy of*  
487 *Sciences* 106, 19685–19692

488 51 Cavanaugh, K.C. *et al.* (2013) Poleward expansion of mangroves is a threshold  
489 response to decreased frequency of extreme cold events. *Proceedings of the National*  
490 *Academy of Sciences* 111, 723–727

491 52 Anderson, B.J. *et al.* (2009) Dynamics of range margins for metapopulations  
492 under climate change. *Proceedings of the Royal Society B: Biological Sciences* 276,  
493 1415–1420

494 53 Jackson, S.T. and Blois, J.L. (2015) Community ecology in a changing  
495 environment: perspectives from the Quaternary. *Proceedings of the National Academy*

496 *of Sciences* 112, 4915–4921

497 54 Harnik, P.G. *et al.* (2012) Extinctions in ancient and modern seas. *Trends in*  
498 *Ecology & Evolution* 27, 608–617

499 55 Barnosky, A.D. *et al.* (2011) Has the Earth’s sixth mass extinction already  
500 arrived? *Nature* 471, 51–57

501 56 Young, H.S. *et al.* (2016) Patterns, Causes, and Consequences of Anthropocene  
502 Defaunation. *Annual Review of Ecology, Evolution, and Systematics* 47, 333–358

503 57 Pounds, J.A. (2006) Widespread amphibian extinctions from epidemic disease  
504 driven by global warming. *Nature* 439, 161–167

505 58 Wiens, J.J. (2016) Climate-Related Local Extinctions Are Already Widespread  
506 among Plant and Animal Species. *PLOS Biology* 14, e2001104

507 59 Scheffers, B.R. *et al.* (2016) The broad footprint of climate change from genes  
508 to biomes to people. *Science* 354, aaf7671

509 60 Veron, J.E.N. (2008) Mass extinctions and ocean acidification: biological  
510 constraints on geological dilemmas. *Coral Reefs* 27, 459–472

511 61 Foote, A.D. *et al.* (2011) Out of the Pacific and Back Again: Insights into the  
512 Matrilineal History of Pacific Killer Whale Ecotypes. *PLoS ONE* 6, e24980

513 62 Chevin, L.-M. *et al.* (2013) Phenotypic plasticity and evolutionary demographic  
514 responses to climate change: taking theory out to the field. *Functional Ecology* 27, 967–  
515 979

516 63 Colwell, R.K. and Rangel, T.F. (2010) A stochastic, evolutionary model for  
517 range shifts and richness on tropical elevational gradients under Quaternary glacial  
518 cycles. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365,  
519 3695–3707

520 64 Quintero, I. and Wiens, J.J. (2013) Rates of projected climate change

521 dramatically exceed past rates of climatic niche evolution among vertebrate species.  
522 *Ecology Letters* 16, 1095–1103

523 65 Morlon, H. (2014) Phylogenetic approaches for studying diversification.  
524 *Ecology Letters* 17, 508–525

525 66 Clavel, J. and Morlon, H. (2017) Accelerated body size evolution during cold  
526 climatic periods in the Cenozoic. *Proceedings of the National Academy of Sciences* 114,  
527 4183–4188

528 67 Manceau, M. *et al.* (2017) A unifying comparative phylogenetic framework  
529 including traits coevolving across interacting lineages. *Systematic Biology* 66, 551–568

530 68 Lewitus, E. and Morlon, H. (2018) Detecting environment-dependent  
531 diversification from phylogenies: a simulation study and some empirical illustrations.  
532 *Systematic Biology* 67, 576–593

533 69 Papadopoulou, A. and Knowles, L.L. (2016) Toward a paradigm shift in  
534 comparative phylogeography driven by trait-based hypotheses. *Proceedings of the*  
535 *National Academy of Sciences* 113, 8018–8024

536 70 Hoffmann, A.A. and Sgrò, C.M. (2011) Climate change and evolutionary  
537 adaptation. *Nature* 470, 479–485

538 71 Angert, A.L. *et al.* (2011) Do species' traits predict recent shifts at expanding  
539 range edges? *Ecology Letters* 14, 677–689

540 72 MacLean, S.A. and Beissinger, S.R. (2017) Species' traits as predictors of range  
541 shifts under contemporary climate change: A review and meta-analysis. *Global Change*  
542 *Biology* 23, 4094–4105

543 73 Estrada, A. *et al.* (2016) Usefulness of Species Traits in Predicting Range Shifts.  
544 *Trends in Ecology & Evolution* 31, 190–203

545 74 Clark, J.S. (2003) Estimating population spread: what can we forecast and how

546 well? *Ecology* 84, 1979–1988

547 75 Díez-del-Molino, D. *et al.* (2018) Quantifying Temporal Genomic Erosion in  
548 Endangered Species. *Trends in Ecology & Evolution* 33, 176–185

549 76 Nogués-Bravo, D. *et al.* (2016) Amplified plant turnover in response to climate  
550 change forecast by Late Quaternary records. *Nature Climate Change* 6, 1115–1119

551 77 Fordham, D.A. *et al.* (2014) Better forecasts of range dynamics using genetic  
552 data. *Trends in Ecology & Evolution* 29, 436–443

553 78 Nogués-Bravo, D. and Rahbek, C. (2011) Communities Under Climate Change.  
554 *Science* 334, 1070–1071

555 79 Franks, S.J. *et al.* (2018) Using the resurrection approach to understand  
556 contemporary evolution in changing environments. *Evolutionary Applications* 11, 17–  
557 28

558 80 Weider, L.J. *et al.* (2018) Evolutionary aspects of resurrection ecology:  
559 Progress, scope, and applications-An overview. *Evolutionary Applications* 11, 3–10

560 81 Frisch, D. *et al.* (2014) A millennial-scale chronicle of evolutionary responses to  
561 cultural eutrophication in *Daphnia*. *Ecology Letters* 17, 360–368

562 82 Orsini, L. *et al.* (2012) The role of selection in driving landscape genomic  
563 structure of the waterflea *Daphnia magna*. *Molecular Ecology* 22, 583–601

564 83 Etterson, J.R. *et al.* (2016) Project Baseline: An unprecedented resource to study  
565 plant evolution across space and time. *American Journal of Botany* 103, 164–173

566 84 Urban, M. (2016) Improving the forecast for biodiversity under climate change.  
567 *Science* 353, 8466

568 85 Swetnam, T.W. and Betancourt, J.L. (1998) Mesoscale Disturbance and  
569 Ecological Response to Decadal Climatic Variability in the American Southwest.  
570 *Journal of Climate* 11, 3128–3147

571 86 Brown, P.M. (2006) Climate effects on fire regimes and tree recruitment in  
572 black hills ponderosa pine forests. *Ecology* 87, 2500–2510

573 87 Gray, S.T. *et al.* (2006) Role of multidecadal climate variability in a range  
574 extension of pinyon pine. *Ecology* 87, 1124–1130

575 88 Lesser, M.R. and Jackson, S.T. (2012) Contributions of long-distance dispersal  
576 to population growth in colonising *Pinus ponderosa* populations. *Ecology Letters* 16,  
577 380–389

578 89 Lesser, M.R. and Jackson, S.T. (2012) Making a stand: five centuries of  
579 population growth in colonizing populations of *Pinus ponderosa*. *Ecology* 93, 1071–  
580 1081

581 90 Lesser, M.R. *et al.* (2013) Development of genetic diversity, differentiation and  
582 structure over 500 years in four ponderosa pine populations. *Molecular Ecology* 22,  
583 2640–2652

584 91 Bush, A. *et al.* (2016) Incorporating evolutionary adaptation in species  
585 distribution modelling reduces projected vulnerability to climate change. *Ecology*  
586 *Letters* 19, 1468–1478

587 92 Miner, B.E. *et al.* (2012) Linking genes to communities and ecosystems:  
588 *Daphnia* as an ecogenomic model. *Proceedings of the Royal Society B: Biological*  
589 *Sciences* 279, 1873–1882

590 93 Dobrowski, S.Z. *et al.* (2011) Modeling plant ranges over 75 years of climate  
591 change in California, USA: temporal transferability and species traits. *Ecological*  
592 *Monographs* 81, 241–257

593 94 Morueta-Holme, N. *et al.* (2015) Strong upslope shifts in Chimborazo’s  
594 vegetation over two centuries since Humboldt. *Proceedings of the National Academy of*  
595 *Sciences* 112, 12741–12745



596 95 Hédl, R. *et al.* (2017) Resurvey of historical vegetation plots: a tool for  
597 understanding long-term dynamics of plant communities. *Applied Vegetation Science*  
598 20, 161–163

599 96 Stewart, J.A.E. *et al.* (2015) Revisiting the past to foretell the future: summer  
600 temperature and habitat area predict pika extirpations in California. *Journal of*  
601 *Biogeography* 42, 880–890

602 97 McInerney, F.A. and Wing, S.L. (2011) The Paleocene-Eocene Thermal  
603 Maximum: A Perturbation of Carbon Cycle, Climate, and Biosphere with Implications  
604 for the Future. *Annual Review of Earth and Planetary Sciences* 39, 489–516

605 98 Prothero, D.R. and Berggren, W.A., eds. (1992) *Eocene-Oligocene Climatic and*  
606 *Biotic Evolution*, Princeton University Press.

607 99 Erdei, B. *et al.* (2007) Neogene flora and vegetation development of the  
608 Pannonian domain in relation to palaeoclimate and palaeogeography. *Palaeogeography,*  
609 *Palaeoclimatology, Palaeoecology* 253, 115–140

610 100 Svenning, J.-C. (2003) Deterministic Plio-Pleistocene extinctions in the  
611 European cool-temperate tree flora. *Ecology Letters* 6, 646–653

612 101 Davis, M.B. and Shaw, R.G. (2001) Range shifts and adaptive responses to  
613 Quaternary climate change. *Science* 292, 673–679

614 102 Hansen, J. *et al.* (2013) Climate sensitivity, sea level and atmospheric carbon  
615 dioxide. *Philosophical Transactions of the Royal Society A: Mathematical, Physical*  
616 *and Engineering Sciences* 371, 20120294–20120294

617 103 Connolly, S.R. *et al.* (2017) Process, Mechanism, and Modeling in  
618 Macroecology. *Trends in Ecology & Evolution* 32, 835–844

619 104 Fordham, D.A. (2016) Predicting and mitigating future biodiversity loss using  
620 long-term ecological proxies. *Nature Clim. Change* 6, 909–916

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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.

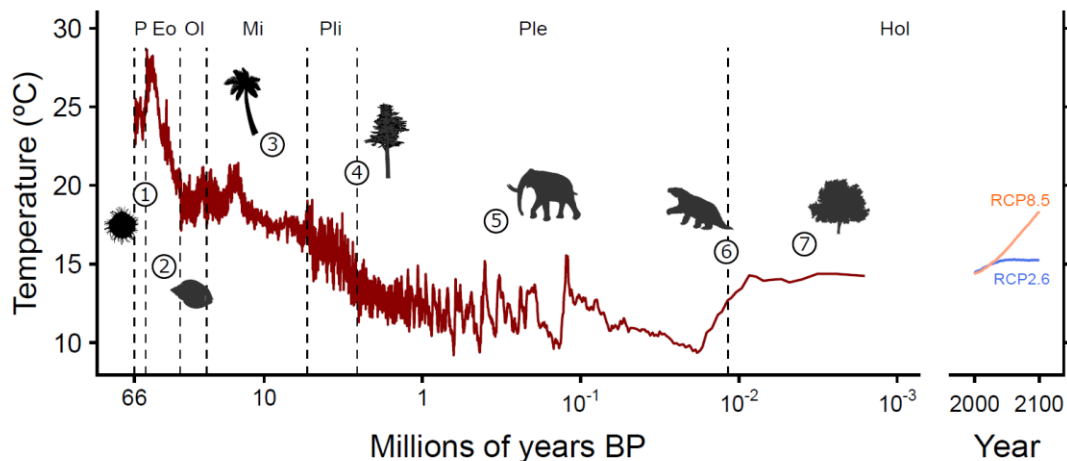
643 **Process-based models** - Spatially explicit approaches that simulate the effect of climate and  
644 environmental conditions on important vital rates (including population growth, dispersal and  
645 plasticity in demographic traits) to explain species distributions and their changes, including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

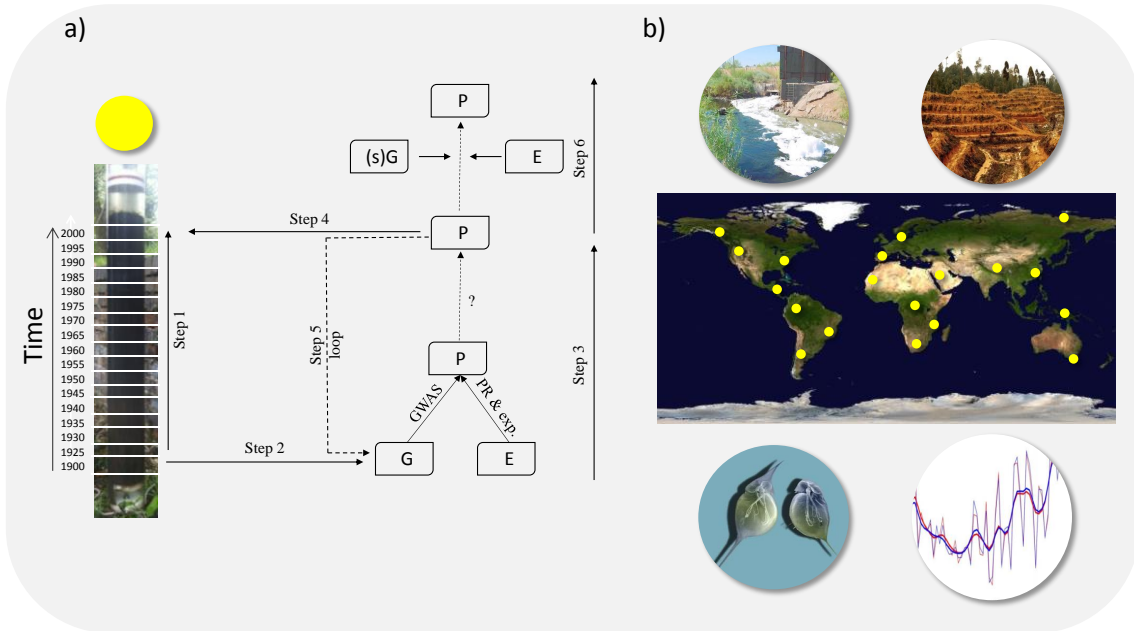
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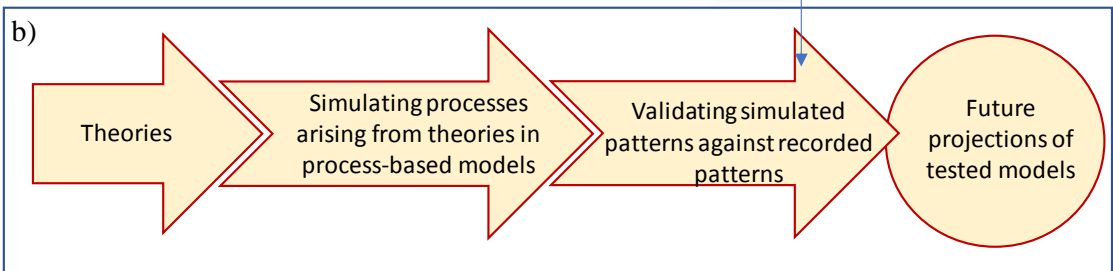
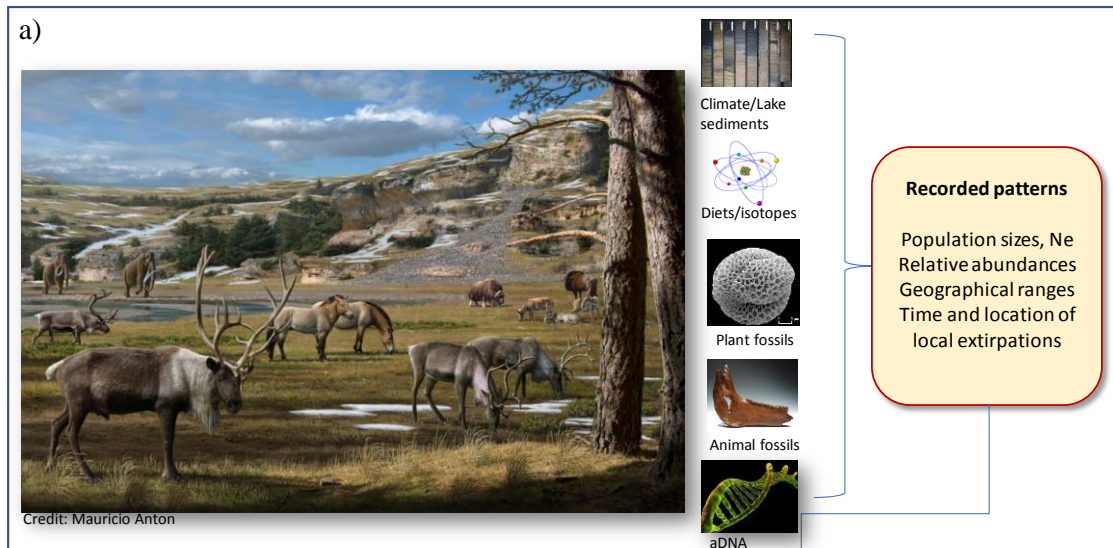
736 **Figure 1. Reconstructing historical patterns of evolutionary change for unravelling**  
737 **mechanisms of genetic and plastic response to anthropogenic environmental**  
738 **changes. a)** Conceptual framework for the integration of resurrection ecology and  
739 predictive models. Using for 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