David Nogués-Bravo, Francisco Rodríguez-Sánchez, Luisa Orsini, Erik de Boer, Roland Jansson, Helene Morlon, Damien A. Fordham, Stephen T. Jackson, Cracking the Code of Biodiversity Responses to Past Climate Change, **Trends in Ecology & Evolution**, Volume 33, Issue 10, 2018, Pages 765-776, https://doi.org/10.1016/j.tree.2018.07.005.

Cracking the code of past biodiversity responses to climate change

Nogués-Bravo, David[1,*], Rodríguez-Sánchez, Francisco[2], Orsini, Luisa[3], de Boer, Erik[4], Jansson, Roland[5], Morlon, Hélene[6], Fordham, Damien A.[7], & Jackson, Stephen T.[8,9]

[1] Center for Macroecology, Evolution and Climate. Natural History Museum of Denmark. University of Copenhagen. Universitetsparken 15, Copenhagen, DK-2100, Denmark.

[2] Departamento de Ecología Integrativa, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Avda. Américo Vespucio 26, E-41092 Sevilla, Spain.

[3] School of Biosciences, University of Birmingham. Edgbaston, Birmingham, B15 2TT, United Kingdom.

[4] Institute of Earth Sciences Jaume Almera, Consejo Superior de Investigaciones Científicas, C/Lluís Solé i Sabarís s/n, 08028 Barcelona, Spain.

[5] Department of Ecology and Environmental Science, Umeå University, Uminova Science Park, Tvistevägen 48, Umeå, Sweden.

[6] Institut de Biologie, Ecole Normale Supérieure, UMR 8197 CNRS, Paris, France.

[7] The Environment Institute, School of Earth and Environmental Sciences, The University of Adelaide, South Australia 5005,Australia.

[8] Southwest Climate Science Center, US Geological Survey, Tucson, AZ 85719, USA.

[9] Department of Geosciences and School of Natural Resources and Environment, University of Arizona, Tucson, AZ 85721.

*Corresponding author: Nogués-Bravo, D. (dnogues@snm.ku.dk)

Keywords: **adaptation, dispersal, extinction, global change, natural experiments, prediction**

Ecologists are increasingly interested in understanding and predicting how biological diversity will respond to climate change. In this context, past biodiversity dynamics recorded in paleo-archives show a broad array of responses, including tolerance, microevolution, migration, and extinction, occurring across a broad range of taxonomic, temporal and spatial scales. However, this accumulated knowledge is largely fragmented within disciplinary and scale boundaries, and synthesis and integration across disciplines are still lacking. Significant knowledge gaps center on the relative roles of evolutionary adaptation, phenotypic plasticity, and dispersal for surviving climate change. Application of paleo-archives offers great opportunities to understand biodiversity responses to future climate change, but also poses challenges for both the paleoecological and global change communities. We outline cross-disciplinary approaches that will better apprehend the mechanisms allowing species to survive, facilitating prediction of future changes in biological diversity.

Does the future of biodiversity lie in the past?

Atmospheric CO_2 levels may rise up to 450-500 ppm by the end of this century, driving an increase in global average temperature on the order of 2 to 5 ºC [1], with future climate forcing potentially without precedent in the last 420 million years [2]. Projected magnitudes and rates of future climate change pose major threats to biodiversity [3-8], and the scientific community is struggling to fully apprehend gross and net responses of biodiversity to climate change, anticipate whether species can respond quickly enough, and pinpoint the various roles of life-history properties (e.g., dispersal, genetic diversity, reproductive strategies, phenotypic plasticity, population growth rates) in adapting to a changing environment. In this context, scientists are looking to the past, using geo-historical records to learn how individuals, populations, communities and biomes have responded to climatic changes [9-22]. Whether individuals and populations will adapt by evolutionary change or plasticity, whether they will migrate fast enough, and whether those responses will be adequate to forestall collapses of species ranges and prevent widespread species extinctions can be explored using case studies from the past. Indeed, past climate change, whether abrupt or gradual, and whether occurring in deep time or recent history, offers a vast set of unplanned natural experiments to explore biodiversity responses and test ecological and evolutionary theories. Recent years have seen the accumulation of well-documented examples of the influence of climate-change on persistence, adaptation and diversification, dispersal, and extinction [11-15, 23]. The effect of climate change on migration rates and routes have been intensively studied by biogeographers and palaeoecologists, augmented recently by molecular markers and ancient DNA (aDNA). *In situ* tolerance to changing climate conditions has been explored in the fossil record using functional morphology, ecophysiology, evolutionary genetics, and developmental plasticity, including recent experimental approaches (e.g., 'resurrection ecology'; [24,25]). Finally, paleoecological records of population extirpations and species extinctions provide information on the nature and consequences of failure of tolerance, evolution, or migration [26,27].

However, key knowledge gaps remain. The relative importance of different mechanisms for persistence (e.g., evolutionary adaptive change versus phenotypic plasticity), and the nature and rates of climate-driven anagenetic and cladogenetic evolution remain poorly understood. The relative efficacy of *in situ* tolerance and migration under different rates and magnitudes of climate change is obscure. Although much attention has been devoted to paleoecological records of migration, rates and underlying controls are not clear except in a few specific cases. Moreover, significant challenges remain for better integrating knowledge, scales, methods and data from a variety of biological disciplines, from paleoecology to genomics. In this review, we (1) synthesize the modal responses of biodiversity to past climate change from deep to recent time (tolerance, migration, and their simultaneous failure, resulting in extinction), (2) identify key knowledge gaps concerning underlying mechanisms (which span a broad set of biological disciplines), and (3) identify and advocate for new approaches that integrate multiple methods and disciplines to better apprehend the strategies of life to adapt to climate change and for anticipating future responses of biological diversity.

Biodiversity responses to climate change

Tolerance, Adaptive Evolution, and Diversification

Biotic adaptation responses to climatic and environmental changes as shown by paleoarchives vary from macroevolutionary divergences (at very long (10^6-10^7 yr) time scales to adaptive evolution (10^0-10^5 yr) to phenotypic adjustments in place (10^{-1}-10^3 yr). Long-term climate change has been considered an important driver of high-order diversification, as clades respond to new climatic regimes, although its effects vary with timespan, habitat, and clade (e.g., marine bivalves [28]) and North American mammals ([29]), and more generally with the ecology of individual species (e.g., Cenozoic macroperforate planktonic foraminifera [30]). In shorter time spans, many individuals and populations can tolerate a high degree of climate change in situ. Some long-lived modular organisms (e.g., corals, plant genets) can survive in place for centuries or even millennia, spanning a broad range of climate change and variation from interannual to millennial [31-33]. Some species have persisted in place since before the last glacial maximum 21,000 years ago; well-documented paleoecological cases include woody plant species in central Europe [34,35], and in unglaciated sections of North America, both eastern [33] and western [36-38].

The paleo genetic records indicate also that adaptive evolution can support long-term persistence of clades in response to climate change [39]. Adaptations can enable exploitation of new niches: Adaptive mutations in woolly mammoth haemoglobin allowed the exploitation of high-latitude cold environments during the Pleistocene [40]. Similarly, the genome comparison of brown bears and polar bears revealed that over half million years, natural selection drove major changes in polar bear genes related to fat transport in the blood and fatty acid metabolism [41]. Moreover, faster traces of microevolutionary changes are recorded in Przewalski's horses after they occupied Yakutia some centuries ago, following the migration of the Yakut people and adapting to severe cold climate [42]. In more recent periods of time, examples of microevolutionary responses to climatic change include changes in the body color of owls during warmer winters [43], or adaptive changes in the flowering time of Brassicas in response to drought [44].

Whether adaptive evolutionary change or plasticity are the prevalent strategy to adapt in situ to climate change, and at what spatial and time frame these two processes play a role, can be difficult to disentangle for extant populations and even more challenging for ancient extinct populations, but both have doubtless been key processes in population persistence under climate change[45]. For most reported cases of climate-driven phenotypic changes in the wild, it remains unclear whether they are caused by microevolution or phenotypic plasticity, although recent meta-analyses [45, 46] suggest that most responses to climatic change are mediated by phenotypic plasticity (see also [47-50]).

Migration

Migration has been a dominant response of species to climate shifts in the past [51]. Past migrations are typically inferred from spatial and temporal patterns in fossil data [52,53], geographic patterns in genetic markers of extant and extinct populations [54], or both (55). The fossil record has indeed provided abundant evidence of (mostly) poleward migration of many species following warming of the Paleocene-Eocene Thermal Maximum [56], or equatorward expansion of plant cold-adapted species during the late-Tertiary global cooling [57]. Likewise, both fossil and genetic approaches indicate (mostly) poleward migrations since the last glacial maximum [51, 54].

Behind these general trends lay multiple different specific species trajectories when migrating. The best knowledge on past migration comes from trees, particularly in Europe and North America during the postglacial period, thanks to extensive fossil records and phylogeographic studies (e.g. 35, 55, 58). These studies reveal variable migration patterns and rates among species, and even within populations of the same species [59], but typical migration rates for the last deglaciation range from a few tens to a few thousand m/yr, with averages around 2.7 km/decade [60-62]. Actual rates may however have been much lower after accounting for refugial populations relatively close to ice sheets [63,64] –but the distribution and frequency of such ‘cryptic’ refugial populations remains under debate [65]. Overall, there is evidence of both high migration rates –including fast responses to abrupt climate change [66]– as well as many species lagging behind climate [67], reinforcing the high specificity of migration patterns across taxa.

There are many different mechanisms by which climate change influences range shifts. First, climate change can improve suitability beyond the range limit so that species may establish at formerly unsuitable areas [68]. Hence, warming would promote expansion of cold-limited taxa towards higher latitudes or altitudes [3,69]. Second, climate change could foster colonisation of new areas in several ways: enhanced fecundity of source populations (thus increasing propagule pressure), increased propensity to disperse or emigrate (in animals), or acceleration of dispersal processes [70]. Climate change can also enhance establishment of propagules after arrival, both directly [71] and (particularly in rapid climate change) by reducing populations of dominant species, via mortality or disturbance [72]. Finally, climate change could reduce the probability of extinction of leading edge populations, for instance due to extreme climatic events [73]. A variety of processes are involved in species migrations and range shifts, all of which can be directly or indirectly (e.g. mediated by species interactions) influenced by climate change [72, 74-76]. A challenge for ecologists, biogeographers, and paleoecologists is to identify generalizations, and to understand the role of species-specific, locale-specific, and time-specific contingencies and idiosyncracies in driving patterns and rates of migration.

Extinction

When species cannot tolerate climate change in situ, or colonize suitable habitat elsewhere quickly enough, they become extinct. In extreme cases, many high-order clades can be lost in mass extinction events. The Earth has indeed witnessed five such events in the last 500 million years, in connection partly with intense climatic changes, both cooling (i.e., End-Ordovician) and warming (i.e., end Triassic), with estimated species losses ranging from 75%, in the Devonian, to 95% (Permian) [12,77]. More recently, the cooling at the inception of the Quaternary caused regional extinctions of many taxa [78]. The Quaternary has also witnessed major environmental changes, with intense climatic shifts between cold and warm periods occurring, on occasions, within a few decades [80,81]. The last deglaciation coincided with the disappearance of many large mammals, with the magnitude of climatic versus anthropic impacts still being hotly debated [27,82]. In contrast there are few documented cases of global plant extinctions through the Pleistocene. However, extinct taxa may leave few traces in the fossil record [83], and macrofossil analysis – often needed to determine species-level differentiation – reveals that plant extinctions may have been more common than assumed [e.g. 26. Similarly, recent studies document species losses of amphibians and reptiles [84], and taxa in the marine realm [85], which were thought to have been relatively stable during the Pleistocene (e.g. herpetofaunal stability hypothesis). Evidence that historic climate shifts (which are small compared to those that occurred during the glacial inter-glacial cycles of the past) drove species extinctions is limited [86], with rare exceptions being synergistic functions of both 20th century human-induced climate change and other proximate drivers of extinction (including infectious diseases) [87]. However, anthropogenic climate disruption is predicted to soon compete with habitat destruction as the most important driver of contemporary extinctions [88,89].

Climate change may trigger extinctions and local extirpations by surpassing the physiological limits of species, by reducing primary productivity of ecosystems and thereby local population fitness across food webs, and indirectly by disrupting ecological interactions via changes in species distributions or phenology. For instance, coral bleaching, the loss of intracellular endosymbionts due to the increase in frequency of extreme heating episodes and changes in the carbon cycle are one of the main supported mechanisms behind coral extinctions during the five mass extinction events [90]. Also, drier and colder climatic conditions during the LGM triggered a reduction in overall primary productivity, provoking losses in genetic diversity and populations of large grazers [13] , depleting lineages, for example, of bowhead whales [91], and contributing to local and global extinctions [27]. These pathways to extinctions in different periods of the Earth’s history share some commonalities. In particular, climatic changes that exceed in magnitude and speed experienced during the evolutionary history of species usually trigger extinction events [92], and climate change has frequently interacted with other extinction drivers.

Unknowns, challenges and routes ahead

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

Evolutionary adaptation versus plasticity?

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

Comparative phylogenetics and novel macroevolutionary approaches are offering new insights into speciation and phenotypic change in response to major climatic shifts [94]. Comparative approaches allow fitting various models of phenotypic evolution and diversification to phylogenies in order to estimate evolutionary rates, including speciation and extinction [14]. Recently, models that can explicitly test for the effect of climatic changes on these evolutionary rates have been developed [95-98].With advances in genomics, particularly methods for treating minute and degraded samples, new critical sources of information will become available. For example, full genomes for thousands of bird species are being sequenced [99], which will reveal macroevolutionary consequences of past climate change and dynamics of effective population sizes, and link them to climatic changes over millions of years [100].

Spatial analysis of species and populations provide important insights into the evolutionary processes that led to present day genetic and phenotypic diversity. However, when limited to exploring current patterns, these analyses are not suitable to measure past processes. Past evolutionary events can be inferred from molecular data, but these events may be confounded by phylogeographic signals, complicating identification of the causes of adaptive and demographic changes. Conversely, long-term observational studies enable measurement of evolutionary processes by comparing temporal changes in genetic and phenotypic diversity with expectations of neutral and adaptive evolutionary models. Long-term studies, however, may require commitments beyond the career or life spans of individual researchers. 'Resurrection Ecology' (see Glossary) provides an alternative path to reconstructing long-term patterns of evolutionary changes and unraveling mechanisms of response to climatic and other environmental changes [19]. Many life forms (zooplankton, insects, algae, fungi, bacteria, plants) produce resting stages as part of their life cycles in response to environmental hardship. When such resting stages can be recovered from ancient sediments and reared in the laboratory, they can reveal molecular targets (genes, metabolites, proteins) that enable evolution and adaptation to changing climate. Resurrecting individuals from such species and populations across documented temporal shifts in environment uniquely permits simultaneous measurement of both plastic (phenotypic and behavioural) and genetic (evolutionary) responses to climatic change, using common garden or transplant experiments [101,102]. Relative fitness of both historical and modern populations can be measured in response to different climatic regimes, including past, present and future. Such long-term studies, replicated across multiple environments and taxa, can be a powerful resource for building models to forecast species persistence [103] (Figure 2).

Migrating fast enough?

Although migration is a key process underlying range shifts and the spread of native and invasive species, the migration capacity of species under rapid climate change remains uncertain (75). While some taxa seem unable to shift ranges under changing climates (67), others seem able to migrate at a fast pace [3]. Attempts to explain observed range shifts based on species traits or ecological strategies have obtained modest results [104,105; but see 106). Low predictability may be expected given the large number of processes involved in range shifts, as well as the complexity and path-dependence when those processes interact. The dispersal process itself is highly stochastic and inherently uncertain [107]. Other important processes include size and fecundity of source populations (which determine propagule pressure), gene flow, local adaptation, evolution of dispersal, biotic interactions (competition, facilitation, mutualisms), Allee effects, and so on, all of which are likely to be affected by climate change as well [75]. Spatial heterogeneity on the landscape plays a role (e.g., dispersal-target size), as does high-frequency climate variability [58, 72]. As a result, we may not be able to go much farther than estimating dispersal potentials for different species or populations [107]. A critical challenge is to use paleoecological and ecological data to identify generalizations that can emerge from the location-specific, species-specific, and event-specific particulars of detailed case studies [58,72].

Paleoecology has largely contributed to estimate how fast species migrated under past climatic changes under minimum levels of pre-historic global human intervention. Unfortunately, contemporaneous dispersal rates are likely to be rather different than past rates due to radically different conditions: more fragmented habitats, missing and novel interactions, or nearly unlimited human-mediated dispersal [75]. Hence, estimates of past migrations rates, however informative, may be of limited value when attempting to forecast future range shifts. Instead, a better understanding of the causes of variation in migration rates may move us forward. Hence, comparative studies of migration patterns among tens or even hundreds of species could throw some light into the role of environmental (contingent) factors as well as intrinsic factors that make some species migrate faster, slower or not at all.

Anticipating future extinctions

Revealing how the accumulative failure of tolerance and migration mechanisms under climate change lead to population extirpation and ultimately species extinction is of utmost importance to provide robust scenarios for future biodiversity and to enhance conservation strategies. Although past extinction events have provided better knowledge on extinction dynamics and their relation to climatic changes, paleo-data together with current data has only recently been fully implemented in quantitative assessments of future risk of extinction [108]. Moreover, correlative approaches lacking key biological mechanisms have dominated the forecasting of future responses of biodiversity to climate change. A large gap remains between mechanistic experiments and large-scale macroecological models that forecast the distribution and persistence of biological diversity under future global climate change [109].

Models that include paleo-dynamics of taxon abundance predict no continental-level extinctions for the end of this century [108], but large changes in the composition of ecological communities, which reflects recorded trends for plants in the Pleistocene. Moreover, a paradigm shift from correlative models of different complexity to mechanistic simulations will bring deeper insights on the interplay of tolerance and migration to explain species range dynamics and extinctions under climate change [20]. Recent insights on the factors correlating with declining genetic diversity, population sizes, and local and global extinctions, have been achieved for megafauna species during the Late Quaternary [13]; but these still are of limited utility for identifying extinction mechanisms. Stochastic process-based models have been used to pinpoint mechanisms driving past changes in species ranges and biological diversity [94,110]. Process-based models applied to explain past recorded changes in biological diversity will improve our ability to explore the role of different mechanisms and explain observed patterns in paleo-archives like species distribution, abundance and genetic diversity [111].

Finally, integration of the genetic level of biodiversity has been recently advocated and holds great potential to include missing mechanisms such as adaptive evolution [20, 105]. Low quality and limited quantity of sample material has impeded application of high-throughput technologies [112] to paleo records. However, recent advances in next-generation sequencing technologies have at least partially mitigated these limitations, allowing extraction of data from small samples and degraded materials, opening a new era for the study of evolutionary processes on macroecological scales (e.g. speciation and extinction of large mammals [113]), as well as at the microecological scale. These technological advances will allow a truly multi-omics approach to identify the molecular targets (proteins, genes and metabolites) driving evolution and speciation at different temporal scales. Long term studies on paleo and neo biological archives, incorporating such approaches as resurrection ecology [19] and experimental macroecology [114] where possible, and combined with spatially explicit mechanistic models, can provide new paths for incorporating eco-evolutionary dynamics in forecast models, and for improving predictions for species survival and persistence under climatic change (see Figure 2).

Concluding remarks

Climate change has triggered large and persistent effects on biological diversity, including speciation, redistribution, local adaptations and extinction events. However, a deeper mechanistic understanding of these dynamics is urgently needed (see also Outstanding Questions). Until recently, lines of evidence have suggested that biotic responses to climate change have been dominated by migration. It is now clear from both paleoecological and ecological perspectives that *in situ* tolerance and adaptative evolution are also key responses to climate change. Although adaptation is now an important object of study, there remain fundamental questions to be addressed: How is adaptive evolution shaped by migration? Conversely, how is migration influenced by adaptive evolution? How do tolerance, adaptive evolution, and migration interact in specific circumstances to reduce or amplify risk of extinction? We advocate for integrating observed long-term responses, paleo experimental arrays, ecological and evolutionary disciplines at macroecological scales (Figure 3). Applying multiomics approaches in paleorecords applied across large spatio-temporal axes has the potential to provide the unique setting to link evolution and migration across long reaches of time, and for a deeper understanding of the roles of adaptation in presence of climate change. Cracking the code of past biodiversity responses to climate change will increase the ability to anticipate responses of biological diversity to climate change.

Acknowledgements

This review emerged from a symposium celebrated at the International Biogeography Society 7th Biennial Meeting in Bayreuth, Germany. D.N.B. thanks Det Frie Forskningsråd (EliteForsk) and the Center for Macroecology, Evolution and Climate. F.R-S. was supported by a postdoctoral fellowship from the Spanish Ministerio de Economía y Competitividad (FPD-2013-16756) and a Severo Ochoa Excellence Award (SEV-2012-0262) to Estación Biológica de Doñana. HM acknowledges support from the European Research Council Grant ERC 616419- PANDA.

References

1 IPCC (2014) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectorial Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, *et al*. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1132 pp.

2 Foster, G. et al. (2017) Future climate forcing potentially without precedent in the last 420 million years. *Nature Communications* 8, 14845

3 Chen, I.-C. et al. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024-1026

4 Moritz, C. et al. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**, 261-264

5 Moritz, C. and Agudo, R. (2013) The future of species under climate change: resilience or decline? *Science* **341**, 504-508

6 García, R.A. et al. (2014) Multiple dimensions of climate change and their implications for biodiversity. *Science* **344**, 6183

7 Urban, M. et al. (2015) Accelerating extinction risk from climate change. S*cience* **353**, aad8466

8 Pecl, G. et al. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* **355**, 6332

9 Jackson, S.T. and Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* **26**, 194–220

10 Willis, K. J. et al. (2010) Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends Ecol. Evol.* **25**, 583-591

11 Dawson, T. P. et al. (2010) Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**, 53-58

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

13 Lorenzen, E.D. et al. (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* **479**, 359-364

14 Condamine, F.L. et al. (2013) Macroevolutionary perspectives to environmental change. *Ecol. Lett.* **16**, 72-85

15 Blois, J. L. et al. (2013) Climate change and the past, present, and future of biotic interactions. *Science* **341**, 499-504

16 Woolbright, S.A. et al. (2014) Climate relicts and their associated communities as natural ecology and evolution laboratories. *Trends Ecol. Evol.* ***29**, 406-416*

17 Brewer, S. et al. (2012) Paleoecoinformatics: applying geohistorical data to ecological questions. *Trends Ecol. Evol.* **27**, 104-112

18 Fritz. S. A. et al. (2013) Diversity in time and space: wanted dead and alive. *Trends Ecol. Evol.* **28**, 509-516

19 Orsini L. et al. (2013) The evolutionary time machine: using dormant propagules to forecast how populations can adapt to changing environments. *Trends Ecol. Evol.* **28**, 274–282

20 Fordham D.A. et al. (2014) Better forecasts of range dynamics using genetic data. *Trends Ecol. Evol.* **29**, 436–443

21 Lamsdell, J.C. et al. (2017) Phylogenetic paleoecology: tree-thinking and ecology in deep time. *Trends Ecol. Evol.* **32**, 452–463

22 Barnosky, A.D. et al. (2017) Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* **355**, eaah4787

23 Franks, J.S. and Hoffmann, A.A. (2012) Genetics of climate change adaptation. *Annu. Rev. Genet.* **46**, 185-208

24 Kerfoot, W. C. and Weider, L. J. (2004) Experimental paleoecology (resurrection ecology): Chasing Van Valen’s Red Queen hypothesis. *Limnol. .Oceanogr.* **49**, 1300-1316

25 Orsini, L. et al. (2016) Temporal genetic stability in natural populations of the waterflea *Daphnia magna* in response to strong selection pressure. *Mol. Ecol.* **25**, 6024–6038

26 Jackson, S.T. and Weng, C. (1999) Late Quaternary extinction of a tree species in eastern North America. *Proc. Nat. Acad. Sci. USA* 96:13847-13852

27 Cooper, A. et al. (2015) Abrupt warming events drove Late Pleistocene Holarctic megafaunal turnover. *Science* **349**, 602–606

28 Huan, S. et al. (2014) Do past climate states influence diversity dynamics and the present-day latitudinal diversity gradient? *Global Ecol. .Biogeogr.* **23**, 530–540

29 Figueirido, B. et al. (2012) Cenozoic climate change influences mammalian evolutionary dynamics. *P. Natl. Acad. Sci. USA* **109**, 722–727

30 Ezard, T.H. et al. (2011) Interplay between changing climate and species' ecology drives macroevolutionary dynamics. Science **332**, 349-51

31 Schulman, E. (1954) Longevity under adversity in conifers. *Science* 119, 396-399

32 de Witte, L.C. and Stöcklin, J. (2010) Longevity of clonal plants: why it matters and how to measure it. *Annals of Botany* **106**, 859-870

33 Roark, E.B., Guilderson, T.P., Dunbar, R.B., Fallon, S.J. & Mucclarone. D.A. (2009) Extreme longevity in proteinaceous deep-sea corals. *PNAS* **106**, 5204-5208

34 Willis, K.J. and van Andel, T.J. (2004) Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quat. Sci. Rev.* **23**, 2369-2387

35 Magri, D. et al. (2006) A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytol.* **171**, 199–221.

36 Nowak, C. L. et al. (1994) A 30 000year record of vegetation dynamics at a semi-arid locale in the Great Basin. J. Veg. Sci. **5**, 579-590

37 Betancourt, J.L. et al. (2001) Late Quaternary vegetation history of Rough Canyon, south-central New Mexico, USA. *Palaeogeogr.Palaeocl.* **165,** 71-95

38 Jackson, S.T. et al. (2005) A 40,000-year woodrat-midden record of vegetational and biogeographic dynamics in northeastern Utah. *J. .Biogeogr.* **32**, 1085-1106

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

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

41 Liu, S. (2014) Population genomics reveal recent speciation and rapid evolutionary adaptation in polar bears. *Cell* **157**, 785-794

42 Librado, P. et al. (2016) Tracking the origins of Yakutian horses and the genetic basis for their fast adaptation. *P. Natl. Acad. Sci. USA* **112**, E6889–E6897

43 Karrel, P. et al. (2011) Climate change drives microevolution in a wild bird. *Nature Communications* **2**, 208

44 Franks, S.J. et al. (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *P. Natl. Acad. Sci. USA* **104**, 1278-1282

45 Merillä, J. and Hendry, A.P. (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol. Appl.* **7**, 1–14

46 Hendry, A.P. et al. (2008) Human influences on rates of phenotypic change in wild populations. *Mol. Ecol.* **17**, 20-29

47 Charmantier, A. et al. (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320, 800-803

48 Charmantier, A. and Gienapp, P. (2014) Climate change and timing of avian breeding and migration: evolutionary *versus* plastic changes. *Evol. Appl.* **7**, 15-28

49 Franks, S.J.et al. (2014) Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evol. Appl.* **7**, 1752-4571

50 Reusch, T.B.H. (2014) Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. *Evol. Appl.* **7**, 123-139

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

52 Huntley, B. and Birks, H. (1984) An atlas of past and present pollen maps for Europe, 0-13,000 years ago, Cambridge University Press.

53 Jackson, S. et al. (1997) Mapped plant-macrofossil and pollen records of late Quaternary vegetation change in Eastern North America. *Quat. Sci. Rev.* 16, 1-70

54 Hewitt, G.M. (2004) Genetic consequences of climatic oscillations in the Quaternary. *Philos. T. Roy. Soc. B* **359**, 183-195

55 Norris, J. et al. (2016) Late Holocene expansion of Ponderosa pine in the central Rockies. *J. Biogeogr*. 43, 778-790.

56 McInerney, A. and Scott L.W. (2011) The Paleocene-Eocene thermal maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annu. Rev. Earth. Planet. Sci.* **39**, 489-516

57 Collinson, M.E. and Hooker, J.J. (2003) Paleogene vegetation of Eurasia: framework for mammalian faunas. *Deinsea* **19**, 41-84

58 Lyford, M. et al. (2003) Influence of landscape structure and climate variability on a late Holocene plant migration. *Ecol. Monogr.* 73, 567-583

59 Lesser, M.R. and Jackson, S.T. (2013) Contributions of long-distance dispersal to population growth in colonizing *Pinus ponderosa* populations. *Ecol. Lett.* 16, 380-389

60 Blois, J.L. (2013) Narrowing the estimates of species migration rates. *Frontiers Biogeogr.* 5, fb_19448

61 Feurdean, A. et al. (2013) Tree migration-rates: narrowing the gap between inferred post-glacial rates and projected rates. *PLoS ONE* 8(8), e71797

62 Ordóñez, A. and Williams, J. (2013) Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecol. Lett.* 16, 773-781

63 McLachlan, J. S. et al. (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, 86: 2088–2098

64 Pearson, R. (2006) Climate change and the migration capacity of species. *Trends Ecol. Evol.* 21, 111-113

65 Tzedakis, P. et al. (2013) Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends Ecol. Evol.* 28, 696-704

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

67 Normand, S. et al. (2011) Postglacial migration supplements climate in determining plant species ranges in Europe. *Proc. R. Soc. B* 278, 3644-3653

68 Holt, R. and Keitt, T. (2000) Alternative causes for range limits: a metapopulation perspective. *Ecol. Lett.* 3, 41-47

69 Hodgson, J.A. et al. (2015) Predicting microscale shifts in the distribution of the butterfly *Plebejus argus* at the northern edge of its range. Ecography 38(10), 998-1005

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

71 Wethey, D. et al. (2011) Response of intertidal populations to climate: Effects of extreme events versus long term change. *J. Exp. Mar. Biol. Ecol.* 400, 132-144

72 Jackson, S. et al. (2009) Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *P. Nat. Acad. Sci. USA* 106, 19685-19692

73 Cavanaugh, K.C. et al. (2014) Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *P. Nat. Acad. Sci. USA* 111: 723-727

74 Anderson, B.J. et al. (2009) Dynamics of range margins for metapopulations under climate change. *Proc. Roy. Soc. B.* 276, 1415-20.

75 Corlett, R. and Westcott, D. (2013) Will plant movements keep up with climate change? *Trends Ecol. Evol.* 28, 482-488

76 Jackson, S. and Blois, J. (2015) Community ecology in a changing environment: Perspectives from the Quaternary. *P. Nat. Acad. Sci. USA* 112, 4915-4921

77 Harnik P.G. et al. (2012) Extinctions in ancient and modern seas. *Trends Ecol. Evol.* **27**, 608-617

78 Svenning, J.-C. (2003) Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecol. Lett.* 6, 646–653

80 Steffensen J.P. et al. (2008) High-resolution Greenland ice core data show abrupt climate change happens in few years. *Science* **321**, 680-684

81 Fordham, D.A. et al. (2017) PaleoView: a tool for generating continuous climate projections spanning the last 21 000 years at regional and global scales. *Ecography,* in press.

82 Saltré, F. et al. (2016) Climate change not to blame for late Quaternary megafauna extinctions in Australia. *Nature Communications* **7**, 10511

83 Plotnick, R.E. et al. (2016) The fossil record of the sixth extinction. *Ecol. Lett.* **19**, 546–553

84 Alroy, J. (2015) Current extinction rates of reptiles and amphibians. *PNAS* **112**, 13003–13008

85 Pandolfi, J.M. et al. (2016). Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**, 955-958.

86 Young, H.S. et al. (2016) Patterns, causes, and consequences of Anthropocene defaunation. *Annu. Rev. Ecol. Evol. Syst.* **47**, 333–5

87 Pounds, J.A. et al. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161-167.

88 Wiens J.J. (2016) Climate-related local extinctions are already widespread among plant and animal species. *PloS Biol.* **14**(12): e2001104

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

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

91 Foote, A.D. et al. (2013) Out of the pacific and back again: insights into the matrilineal history of pacific killer whale ecotypes. *PLoS ONE* 6, e24980

92 Brooks, B.W. et al. (2008) Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453-460

93 Cambronero et al. (in review) Haemoglobin-mediated response to hyper-thermal stress in the keystone species *Daphnia magna*

94 Colwell, R. K.and Rangel, T. F. (2010) A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under Quaternary glacial cycles.*Phil. T. Roy. Soc. B* **365**, 3695–3707

95 Clavel, J. and Morlon, H. (2017) Accelerated body size evolution during cold climatic periods in the Cenozoic. *Proc. Nat. Acad. Sci. USA* **114**, 4183–4188

96 Morlon, H. (2014) Phylogenetic approaches for studying diversification. *Ecol. Lett.* **17**, 508-525

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

98 Lewitus, E. and Morlon, H. (2017) Detecting environment-dependent diversification from phylogenies: a simulation study and some empirical illustrations. *bioRxiv* 162248

99 Zhang, G. et al. (2014) Comparative genomics reveals insights into avian genome evolution and adaptation. *Science* **346**, 1311-1320

100 Nadachowska-Brzyska, K. et al. (2015) Temporal dynamics of avian populations during Pleistocene revealed by whole-genome sequences**.** *Curr. Biol.* **25,** 1375-1380

101 Orsini, L. et al. (2013) The role of selection in driving landscape genomic structure of the waterflea *Daphnia magna. Mol. Ecol.* **22**, 583-601

102 Etterson, J.R. et al.(2016) Project Baseline: An unprecedented resource to study plant evolution across space and time. *Am. J. Bot.* **103**, 164-173

103 Urban, M. et al. (2016) Improving the forecast for biodiversity under climate change. *Science* 353, aad8466

104 Angert, A.L. et al. (2011) Do species' traits predict recent shifts at expanding range edges? *Ecol. Lett.* 14, 677-689

105 MacLean, S.A. and Beissinger, S.R. (2017) Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. Glob. Change Biol., in press

106 Estrada, A. et al. (2016) Usefulness of species traits in predicting range shifts. *Trends Ecol. Evol.* 31, 190-203

107 Clark, J.S. et al. (2003) Estimating population spread: what can we forecast and how well? Ecology 84, 1979-1988

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

109 Nogués-Bravo, D. and Rahbek, C. (2011) Communities under climate change. *Science* **334**, 1070-107

110 Evans, M.E.K. et al. (2016) Towards process-based range modeling of many species. *Trends Ecol. Evol.* **23**, 860-871

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

112 Knapp, M. et al. (2012) Generating barcoded libraries for multiplex high-throughput sequencing. *Mol. Biol.* **840**, 155-170

113 Orlando, L. et al. (2013) Recalibrating *Equus* evolution using the genome sequence of an early Middle Pleistocene horse. Nature **499**, 74–78

114 Alexander, J.M. et al. (2016) when climate reshuffles competitors: a call for experimental macroecology. *Trends Ecol. Evol.* **31**, 831-841

115 Orlando, L. and Cooper, A. (2014) Using ancient DNA to understand evolutionary and ecological processes. *Annu. Rev. Ecol. Evol. Syst.* 45, 573-598

116 Simberloff, D. (1986) The proximate causes of extinction. In: Raup D.M. and Jablonski, D., eds. Patterns and processes in the history of life. Berlin: Springer. pp. 259–76

117 Soulé, M.E. and Wilcox, B.A. (1980) Conservation biology, an evolutionary-ecological perspective. Sunderland: Sinauer Associates.

1181 Hansen, J. et al. (2013) Climate sensitivity, sea level and atmospheric carbon dioxide. *Phil. Trans. R. Soc. A.* 371: 20120294.

119 Prothero, D.R. and Berggren, W.A., eds (1992) *Eocene-Oligocene climatic and biotic evolution*. Princeton University Press.

120 Davis, M.B. and Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science* 292(5517): 673-679.

121 Bakker, E.S. et al. (2016) Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *PNAS* **113**, 847–855

Glossary

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

Dormant propagules – A still living but dormant seed, cyst, spore or egg preserved in ice, soil, sediment, permafrost, or other media.

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

Migration – Spatial displacement of organisms leading to shifts of species distributions with climate change.

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

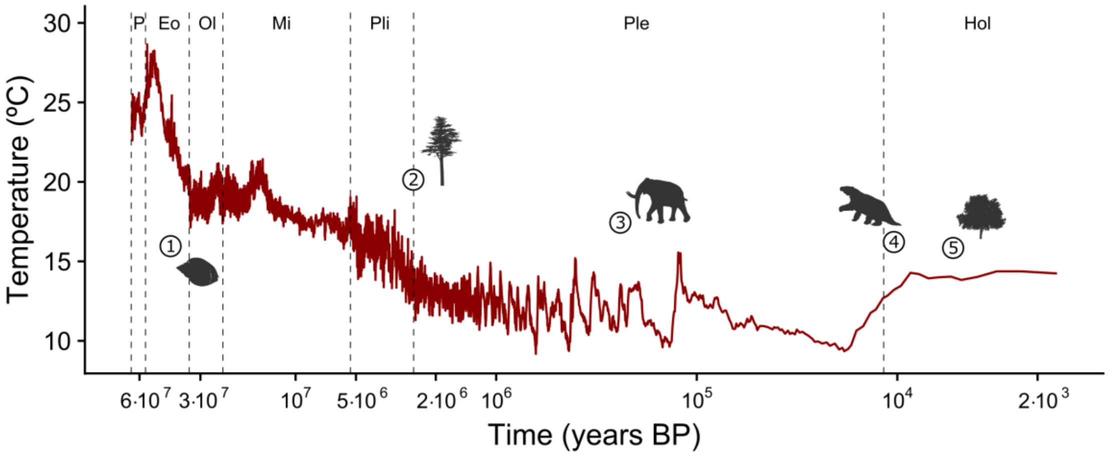
Phenotypic plasticity – Ability of individuals of a genotype to alter physiology, morphology, anatomy, phenology, behaviour, or other phenotypic traits in response to environmental change.

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

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

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

Box 1. Past responses of biological diversity under climate change.



Future climate forcing may surpass those of the previous several million years. Countless individuals in thousands of species across the globe will need to tolerate climate change in situ, disperse and migrate to more suitable climatic conditions, or undergo extinction. Figure 1 highlights a number of biodiversity responses directly or indirectly linked to climatic changes along the Cenozoic (last 65 million years; temperature data from [118]). 1) Under a global cooling trend, winters became >4 °C colder across the Eocene/Oligocene boundary, partially driving extinction of many terrestrial mammals in Europe and marine invertebrates [119]. 2) More than half (52%) of the cool-temperate European tree genera did not survive to the glaciation cycles starting at the end of the Pliocene [78]. 3) An adaptive mutation of haemoglobin enabled mammoths to tolerate the very low temperatures at high latitudes [40]. 4) More than 70% of megafauna genera in the Americas and Australia, and 40% in Eurasia, underwent extinction within a relatively brief period of time (5,000-10,000 years; [12]. 5) Plants in North America migrated northwards between 450 and 2200 km in less than 10,000 years under a warming of 5 degrees [120]. Abbreviations of geological epochs as follows: P = Palaeocene, Eo = Eocene, Ol = Oligocene, Mi = Miocene, Pli = Pliocene, Ple = Pleistocene, Hol = Holocene.

Box 2. Correlations are not enough: experiments and simulations in paleobiology

Much of the evidence for the impact of past climate change on biological diversity is based on patterns of co-occurrence between past climatic events and biological responses as speciation, migration, tolerance and extinction. For deep-time studies the low temporal resolution of available dating techniques creates difficulties in aligning relevant abiotic dynamics (i.e., climate change, acidification, volcanisms) with biological events. Moving from correlations to causation is challenging because of the co-varying climatic variables. Deep-time speciation and extinction events, for example, have been shown to co-occur with both warming and cooling events but also in coincidence with massive CO_2 releases and ocean acidification. Moreover, human impacts during the Late Quaternary have affected biodiversity directly and indirectly, interacting with climate. Exclosure ecological experiments coupled with paleo-ecological data have provided evidence of widespread changes in community composition and ecosystem structure and function due to large herbivore impacts [121] Recently, the use of high throughput sequencing technologies on ancient DNA, the use of paleogenetics, and advances in experimental approaches on living fossils (dormant propagules) have provided important insights into genetic and phenotypic responses to climate change [94]. The discovery of molecular targets (genes, metabolites, proteins) of climate change that enable evolution and adaptation will help unveil mechanisms that contribute to species and population persistence. In parallel, spatial modelling in macroecology can offer more mechanistic insights by switching from correlative models to process-based simulations. Stochastic simulations considering speciation, anagenetic evolution, niche conservatism, range shifts and extinctions [94] are, for example, a promising route to understand the role of those mechanisms in biodiversity responses under climate change. We advocate for the development and further integration of experiments, multi-omics and simulations on paleo-biological systems to better anticipate future responses of biological diversity to climate change.

Box 3. Outstanding Questions

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

-What are the long-term adaptive responses to climate change? Temporal trajectories of fitness changes in response to climatic and anthropogenic changes are paramount [19] to unravel the evolutionary processes leading to population persistence (evolutionary rescue). This knowledge, in turn, is critical to obtain realistic projections of species persistence in future climate change scenarios. Our ability to confidently detect bottlenecks, local extirpation and extinction in response to climatic or anthropogenic changes depends on ability to sample before and after a drastic environmental change took place. The most direct and powerful way to gain such information is by studying species producing dormant propagules (Box 1) that can be sampled across temporal environmental shifts, including climate change [115] .

-Can we predict future extinctions with our current data? Unifying the declining-species paradigm and the small-population paradigm [116,117], which consider both the factors contributing to the general decline of species before their populations become rare, and the genetic and demographic factors promoting the extinction of small populations we can translate and simulate these factors into process-based simulation models. Spatially explicit mechanistic population models that include ecologically important phenotypic traits such as morphology, physiology, phenology, evolutionary adaptive potential, species behaviour and species interactions are a promising route. These types of models are in their infancy because both environmental and empirical ecological variables are needed as prior information to correctly predict future population persistence. We are therefore in much need firstly of more biological and paleobiological data across large climatic and anthropogenic pressure gradients, highlighting the key role field-work, expeditions, biological collections and natural history museums to resolve the relevant societal challenges of the biodiversity crisis.

Fig 2. Reconstructing historical patterns of evolutionary changes and unravels mechanisms of genetic and plastic response to anthropogenic environmental changes. a) Conceptual framework for the integration of resurrection ecology, paleo'omics' and macroecology. Using for example Daphnia as a system, we can resurrect propagules, step 1, an develop a matrix of genotypes (G) and phenotypes (P). Environmental variables (E) are also measured. The matrix of P and G is linked, step 2, via a genome wide association analysis (GWAS) and environmental variables (E) are linked to phenotypes (P) via experimental set ups and paleo records (PR). Using known E and trajectories of G over time, step 3, a model is applied to predict P . The outcome of the model is checked against empirical data, step 4. The model parameters are adjusted, step 5, to reflect real outcomes observed in empirical after several iterations). Using projected E and simulated G ((s)G) from past trajectories future P are predicted with a level of uncertainty . **b)** Scaling up the approach described in a) to a macroecological scale we can identify evolutionary and plastic responses of species to global anthropogenic pressures (within circles from upper left to bottom right: habitat degradation, land-use changes, invasive species and climate change).

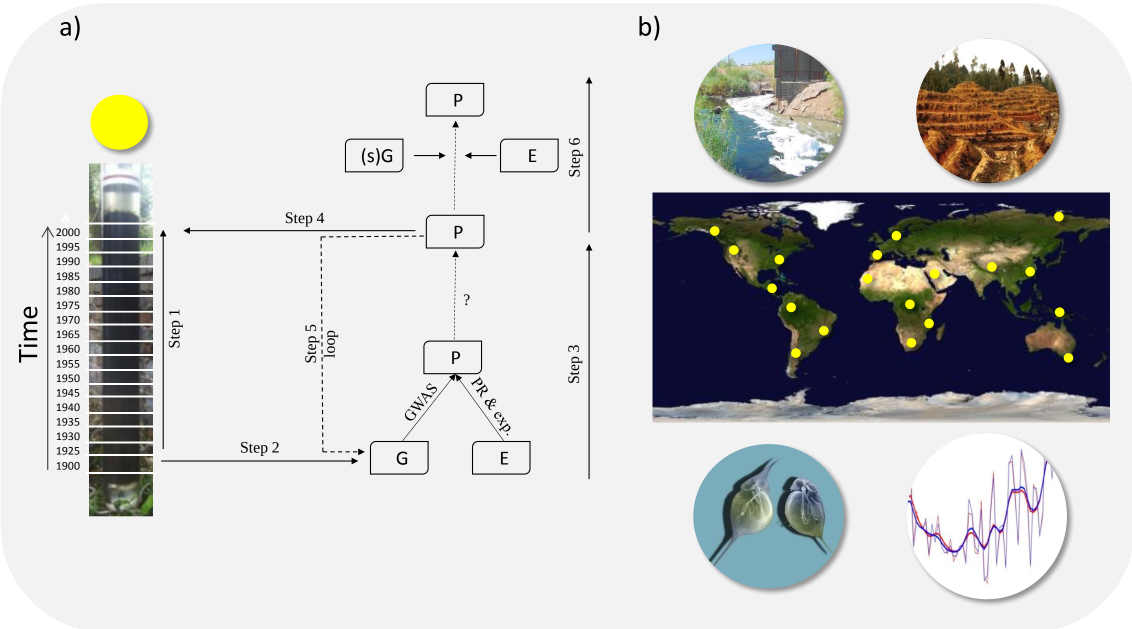


Fig. 3. Cracking the code of biodiversity responses. We identify a series of research challenges, central ring, and disciplines, inner ring, to provide multiple lines of evidences on the past magnitudes, rates and mechanisms of modal biodiversity responses and to inform and feed future biodiversity scenarios.