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# The effect of climate legacies on extinction dynamics: A systematic review

Gregor H. Mathes[1,2,3], Catalina Pimiento[1,4,5], Wolfgang Kiessling[3], Jens-Christian Svenning[6] and Manuel J. Steinbauer[2,7]

[1]Paleontological Institute and Museum, University of Zurich, Zurich, Switzerland; [2]Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany; [3]GeoZentrum Nordbayern, Friedrich-Alexander University Erlangen-Nürnberg (FAU), Erlangen, Germany; [4]Department of Biosciences, Swansea University, Swansea, UK; [5]Smithsonian Tropical Research Institute, Balboa, Panama; [6]Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), Department of Biology, Aarhus University, Aarhus, Denmark and [7]Department of Biological Sciences, University of Bergen, Bergen, Norway

## Review

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**Corresponding author:**
Gregor H. Mathes;
Email: gregorhansmathes@gmail.com

### Abstract

One of the main objectives of ecological research is to enhance our understanding of the processes that lead to species extinction. A potentially crucial extinction pattern is the dependence of contemporary biodiversity dynamics on past climates, also known as "climate legacy". However, the general impact of climate legacy on extinction dynamics is unknown. Here, we conduct a systematic review to summarize the effect of climate legacies on extinction dynamics. We find that few works studying the relationship between extinction dynamics and climate include the potential impact of climate legacies (10%), with even fewer studies reaching beyond merely discussing them (3%). Among the studies that quantified climate legacies, six out of seven reported an improved fit of models to extinction dynamics, with most also describing substantial impacts of legacy effects on extinction risk. These include an increase in extinction risk of up to 40% when temperature changes add to a long-term trend in the same direction, as well as substantial effects on species' adaptations, population dynamics and juvenile recruitment. Various ecological processes have been identified in the literature as potential ways in which climate legacies could affect the vulnerability of modern ecosystems to anthropogenic climate change, including niche conservatism, physiological thresholds, time lags and cascading effects. Overall, we find high agreement that climate legacy is a crucial process shaping extinction dynamics. Incorporating climate legacies in biodiversity assessments could be a key step toward a better understanding of the ecological consequences arising from climate change.

### Impact statement

Our research highlights how past climates, or 'climate legacies,' influence current extinction risks and biodiversity. Through a systematic review across different species and timescales, we show that climate legacies can shape species' adaptations, population trends and juvenile recruitment, ultimately affecting their survival. Understanding this intricate interplay between past climates and present ecosystems is hence crucial for accurately predicting and mitigating the impacts of future climate change on biodiversity. Our study calls on researchers to explore climate legacies more deeply and integrate them into ecological studies, encouraging collaboration between fields like ecology and palaeontology.

## Introduction

Biodiversity faces increasing pressure from various anthropogenic factors (Tilman et al., 2017), with climate change being one of the significant contributors (Wiens, 2016; Pecl et al., 2017). Understanding the processes that drive taxa to extinction through interactions between climate change and the biosphere is a fundamental goal of ecological research and conservation science (Kerr et al., 2007; Brook and Alroy, 2017). A key aspect of this understanding is acknowledging the enduring influence of past climates on present ecosystems.

Traditionally, much focus has been placed on the impact of current abiotic factors on ecological processes. Recently, however, ecologists have improved their understanding of ecological processes by explicitly considering the legacies of past climatic conditions on present systems and processes (Ogle et al., 2015; Svenning et al., 2015; Johnstone et al., 2016), generally termed as "climate legacy". Climate legacies are part of the broader concept of "ecological memory," which encompasses all influences from past processes on present ecosystems (Nyström and Folke, 2001; Folke, 2006; Schweiger et al., 2019). The influence of climate legacies on ecological systems can be expected to be widespread because of the dynamic nature of ecological processes and the inherent complexity and interconnectedness of ecological processes (Ricklefs et al., 1999; Chave, 2013; Ogle et al., 2015; Svenning et al., 2015). Although the magnitude might be strongly scale dependent, the general presence of climate legacies can arise from any length of time in the past (Svenning et al., 2015).

Climate legacies can profoundly mediate a system's response to geologically brief perturbations (Mathes et al., 2021) and could therefore be critically important for understanding how species are responding to climate change. For example, if a particular species has evolved under relatively stable climate conditions, it may be less resilient to sudden or drastic changes in temperature or precipitation due to its narrow niche width (e.g., Janzen, 1967; Grinder and Wiens, 2023). Similarly, if an ecosystem has experienced historical disturbances or fluctuations in climate, these past events may affect its ability to cope with or adapt to present-day climate change. For example, the outcome of the global heat wave on the Great Barrier Reef in 2017 depended not only on the heat stress of that year but also on the history of heat exposure and the physiological and ecological responses experienced in a heat wave 1 year earlier (Hughes et al., 2019). This dependence on historical disturbances or fluctuations in climate can also be observed over coarser timescales, where, for example, Late Quaternary climate velocity is associated with modern endemism (Sandel et al., 2011). Furthermore, the historical assembly of ecological communities might be influenced by past climate conditions, where climate from tens of thousands of years ago influences contemporary functional composition, leading to legacy effects that persist over time (e.g., Blonder et al., 2018). Failing to integrate climate legacies into conservation could thus lead to inaccurate predictions of future extinction patterns. However, a nuanced understanding of the relationship between climatic changes and biotic responses in time, including legacy effects, is currently missing (Bardgett et al., 2005; Crooks, 2005; Resco et al., 2009; Ogle et al., 2015), with the overall effect of climate legacy on extinction dynamics remaining unknown.

Here, we perform a systematic review of the current knowledge on the effect of climate legacies on extinction dynamics. We identify and discuss the climatic processes that could shape extinction risk through climate legacies. By incorporating a range of taxonomic groups and by spanning many magnitudes of temporal scale, our results provide insights into the ecological impact of climate legacy on biodiversity through time. Our findings show that integrating climate legacies in future studies is crucial to provide more accurate predictions of the fate of biodiversity under anthropogenic pressures, particularly climate change.

## Systematic review

We searched for published studies on extinction dynamics linked to climate change on April 6, 2023 on the Web of Science citation database (www.webofknowledge.com) and the Scopus (www.scopus.com) citation database. For this, we used the following keywords:

> (TI=(('extinct*' OR 'extirpat*') AND ('climate change' OR 'changing climate' OR 'temperature'))) AND DT=(Article) for the Web of Science (288 results);
>
> TITLE(("extinct*" OR "extirpat*") AND ("climate change" OR "changing climate" OR "temperature")) AND DOCTYPE(ar) for Scopus (313 results).

This corresponds to a literature search for studies with either extinction or extirpation in combination with climate change or temperature in their title, rather than abstracts or keywords. This restriction was intentional, as it allowed us to conduct a more manageable review by narrowing down to studies most explicitly centered on climate-driven extinction dynamics. However, this approach may have also excluded studies where climate legacy effects are discussed within the text but not emphasized in the title, potentially limiting the comprehensiveness of our review. This trade-off reflects a balance between thoroughness and feasibility, acknowledging that a broader search scope would require significantly more resources and time for screening and analysis. Our findings should therefore be interpreted with this selective focus in mind, as additional studies on climate legacies in extinction may exist beyond the scope of our title-restricted search. We then used the R programming environment R version 4.2.3 (R Core Team, 2023) to identify and eliminate duplicate entries. Additionally, titles were screened to exclude obviously ineligible studies. The filtered dataset contained 351 publications (Figure 1). We excluded articles of languages other than English, German or Spanish, as these were not accessible to the authors. We then manually checked each publication for relevance with the following eligibility criteria:

1. Relevance to climate change and extinction dynamics: The study must investigate the impact of climate change on extinction dynamics, including factors such as habitat loss, range shifts, population declines and extinction risk.
2. Study design: Studies must include empirical research, modeling studies, meta-analyses, longitudinal studies tracking changes in species populations over time, experimental studies, reviews or theoretical analyses. This inclusive approach allows us to capture both empirical findings and conceptual insights, providing a fuller understanding of climate legacy research and highlighting gaps where further empirical study is needed.
3. Methodological rigor: Studies must use scientifically robust methods appropriate to their research question, including clear definitions, reproducible methodologies and valid statistical or modeling approaches and must be peer-reviewed. As such, studies were excluded that did not specify sampling or analytical methods, used unsupported assumptions in models or lacked statistical validation.

Screening was performed concomitantly by the first author (GHM) and a student assistant, wherein the concordance rate of independent decisions was 98%. We addressed instances where decisions differed (i.e., seven publications) through discussion-based sessions aimed at reaching a consensus through the eligibility criteria. Screening resulted in the removal of 144 publications, leaving 207 publications (Figure 1). We then went through each publication and recorded the following meta-data wherever possible: year of publication; biotic unit of the studied taxa (e.g., species, population, etc.); kingdom of the studied taxa; temporal scale of the climate change (e.g., 1 year); methodology used to assess the impact of climatic changes on taxa (e.g., species distribution model, regression model etc.); whether climate legacies were included and quantified; the assumed ecological process of the climate legacy (e.g., migration lags, niche conservatism, etc.); the temporal scale of the climate legacy and the effect size with accompanying type of effect measure (e.g., "spearman's rank correlation coefficient of 1", "percentage change of 20%"). All code and data can be accessed on GitHub (https://github.com/Ischi94/lit_review_past_climate).


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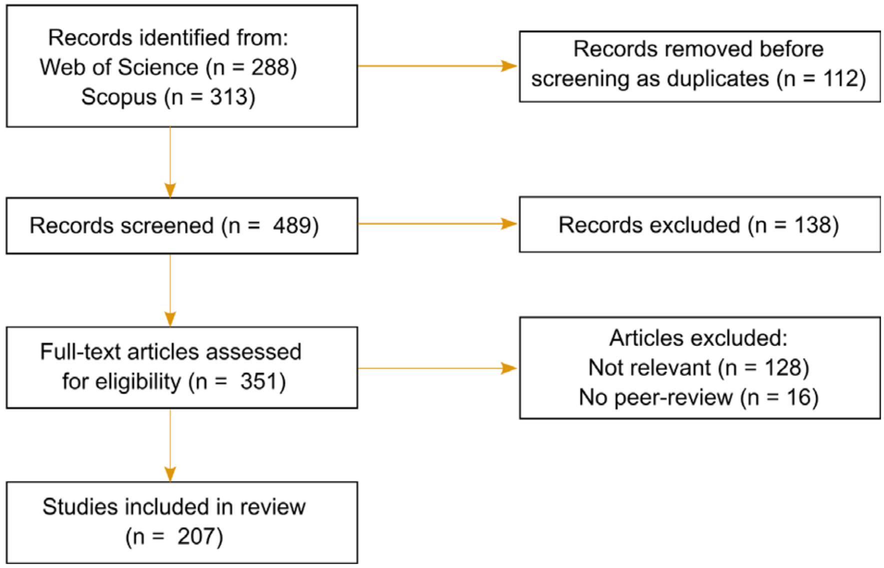


**Figure 1.** Flow diagram depicting the flow of information through the different phases of the systematic review, mapping the number of records identified, included, excluded and the reasons for exclusions.

## Climate legacy impacts on past extinctions

Most of the 207 studies of this systematic review covered either animals (n=137) or plants (n=56), with a few studies on fungi (n=2), protozoans (n=2) or Chromista (n=2). The most common biotic entity was species (n=118), followed by population (n=32) and genus (n=11), and a few studies with tribes (n=1) or individuals (n=1). Five studies used simulated biotic entities (meta-species or meta-populations). The studied extinction response variables in relation to climate change included direct extinction observations from the fossil record, population dynamics such as juvenile recruitment, habitat degradation, changes in species ranges and experimental observations of fitness changes.

Climate legacies were found to act over various temporal scales, ranging from days to millions of years (Figure 2a). However, only 20 studies (10%) included climate legacies either in their methodological framework or in the discussion section (Figure 2). Then, 7 of the 20 studies quantified the effect of the climate legacy on the extinction parameter, whereas the remaining 13 studies discussed the effect of climate legacies qualitatively. We found that the probability of a study including climate legacies either in their methodological framework or in their discussion is growing each year, on average, by 2.3% (95% confidence interval [CI] [−3%, 10%], Figure 2b). Based on this trend, a randomly selected study from 1980, for example, would have a probability of including climate legacies of 5.2% (95%, CI [0%, 16.6%]), whereas a study published in 2023 would have a probability of 13% (95% CI [4.9%, 21%]). This can be attributed to an increasing availability of spatially explicit paleoclimatic data (e.g., Brown et al., 2018), and an increasing focus on understanding the importance of past climates for biodiversity and ecosystem functions (e.g., Svenning et al., 2015).

Including preceding climate estimates among the explanatory variables explained more variance of fossil extinction events than concurrent climate alone, with temperature changes adding to a long-term temperature trend in the same direction (i.e., climate cooling following on a long-term cooling and climate warming following on a long-term warming) being particularly harmful, with an increase in extinction risk of up to 40% (Mathes et al., 2021). However, the legacy effect of temperature on genus extinction risk across the Phanerozoic was found to explain less variance than concurrent temperature alone (Mayhew et al., 2008), and the overall effect of climate on late Quaternary megafauna extinctions in Australia was found to be low, irrespective of whether concurrent climate or climate legacies where used (Saltré et al., 2016), in line with these extinctions being driven by *Homo sapiens* rather than climate (Svenning et al., 2024). High autocorrelation in temperature values on a day-to-day basis was found to significantly affect the population dynamic of bush crickets (Griebeler and Gottschalk, 2000), and existing adaptations to climatic conditions were found to be a strong determinant of temperature-induced extinction risk in Late Quaternary mammals based on simulations (Varela et al., 2015). In addition, the weather conditions of the preceding year determined the juvenile recruitment of whooping cranes (Butler et al., 2017) and the population dynamics of alpine grouses (Imperio et al., 2013).

The remaining 13 studies discussed climate legacies as a potential cause for the extinction measure. Riquelme et al. (2020), for example, discussed how long-term warming affects the carrying capacities and equilibrium densities of populations. In a forest succession model, García-Valdés et al. (2018) showed how climate change-driven extinctions of tree species affect forest functioning more than random extinctions, with the remaining community being more susceptible to future climatic changes. Similarly, climate-induced removal of individuals in ginseng populations was discussed to drive changes in reproductive rates and inbreeding, shaping population functioning (Souther and McGraw, 2014). Urban et al. (2012) examined a cascading dynamic in the response of species to climate change, with competition creating range lags, and those range lags subsequently modifying the ability of the community to respond to further climatic changes. Sax et al. (2013) showed that climatic changes will have a more severe impact on species when previous migration lags have already resulted in species being closer toward the rear edge of their tolerance niche, in line with Hampe and Petit (2005). Similarly, Wiens et al. (2019) found support that montane lizards were isolated by past climate warming and would therefore be highly susceptible to anthropogenic warming.


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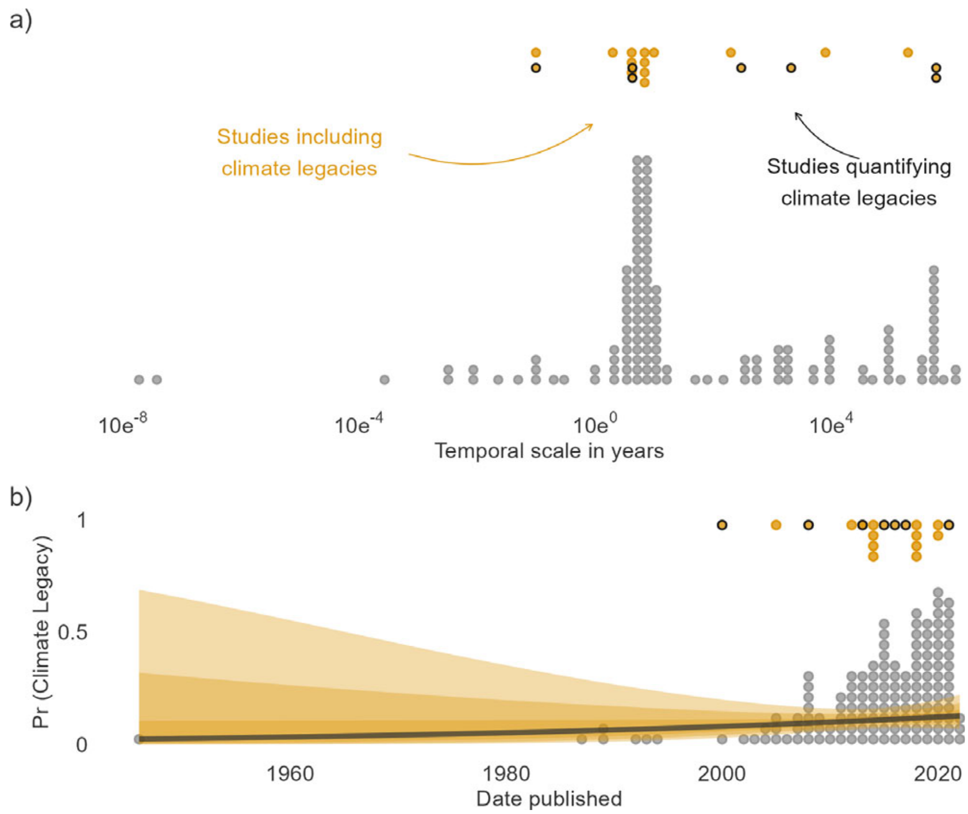


**Figure 2.** Summary of studies including climate legacies. (a) The temporal scale of each study of the systematic literature review on extinction risk and climate change. (b) The temporal trend of the inclusion of climate legacies in studies on extinction risk and climate change. The y-axis shows the probability of climate legacies being included as a function of time. The trend was estimated by a Bayesian logistic regression with non-informative priors. The gray line shows the mean trend, and the yellow shaded areas depicting the 50%, 80% and 95% CIs around this trend. Studies that exclude climate legacies, neither in their methodological framework nor in their discussion, are shown in gray. Studies including climate legacies are shown in yellow. Studies including climate legacies and simultaneously quantifying the effect of these legacies on the extinction parameter are shown in yellow and with a black outline.

## Underlying processes

Although climate legacies can manifest through a range of ecological processes, the examined literature shows that the main processes through which past climate can act on the biosphere and on extinction risk can largely be reflected in three categories: niche conservatism, time lags and tipping points (Figure 3).

(i) Niche conservatism, which is the relative stability of a lineage's niche in spite of evolutionary change (Wiens and Graham, 2005; Hopkins et al., 2014), can generate long-lasting climate legacies in ecological systems (Svenning et al., 2015; Mathes et al., 2021). In these ecological systems, a clear signal of evolutionary rescue (i.e., rapid evolutionary adaptation to climatic change) is rare (Carlson et al., 2014). Fossil studies have similarly shown that the preference of taxa for a particular niche tends to stay constant through time (e.g., Hopkins et al., 2014; Antell et al., 2021). If taxa do not adapt to climatic changes over evolutionary timescales, then these changes will successively move taxa out of their adaptive space (Mathes et al., 2021), particularly in light of climate-related extinction thresholds (Song et al., 2021). Taxa that have experienced but have not adapted to climatic changes are consequently expected to show higher susceptibility to new climatic changes compared to taxa that are in full equilibrium with their adaptation space. Physiological thresholds might be the underlying mechanism for this differential extinction (Calosi et al., 2019), which has been indicated in various experimental settings as well as for extinction events in the fossil record (Reddin et al., 2020). Past climatic changes may have already impacted the fitness of individual taxa, decreasing their tolerance to future climatic changes. This has been shown for pre-existing thermoregulatory adaptations to climate (Sinervo et al., 2018), initial dependency to climate of juvenile recruitment (Butler et al., 2017), susceptibility to drought conditions (Pomara et al., 2014), reproductive success as a function of snow-free grounds in the previous year (Imperio et al., 2013), and growth and reproduction influenced by autocorrelated temperature (Griebeler and Gottschalk, 2000). When taxa keep niche preferences over time, crossing physiological thresholds is therefore more likely if previous climatic changes have impacted taxa negatively (Figure 3b).

(ii) Time lags comprise the amount of time between an extrinsic perturbation to a system and its return to a state of equilibrium (Hastings, 2004), and they can have severe ecological consequences (O'Dea et al., 2007; Svenning and Sandel, 2013; Bunting et al., 2017). For example, climatic changes can cause incomplete range filling and consequently reduce species' geographical distribution ranges (Sandel et al., 2011). Given that small species ranges are associated with increased extinction risk (Davies et al., 2009; Enquist et al., 2019), range truncations due to past climatic changes might shape the response of species to future climatic changes (i.e., increase extinction risk). Similarly, climate-induced


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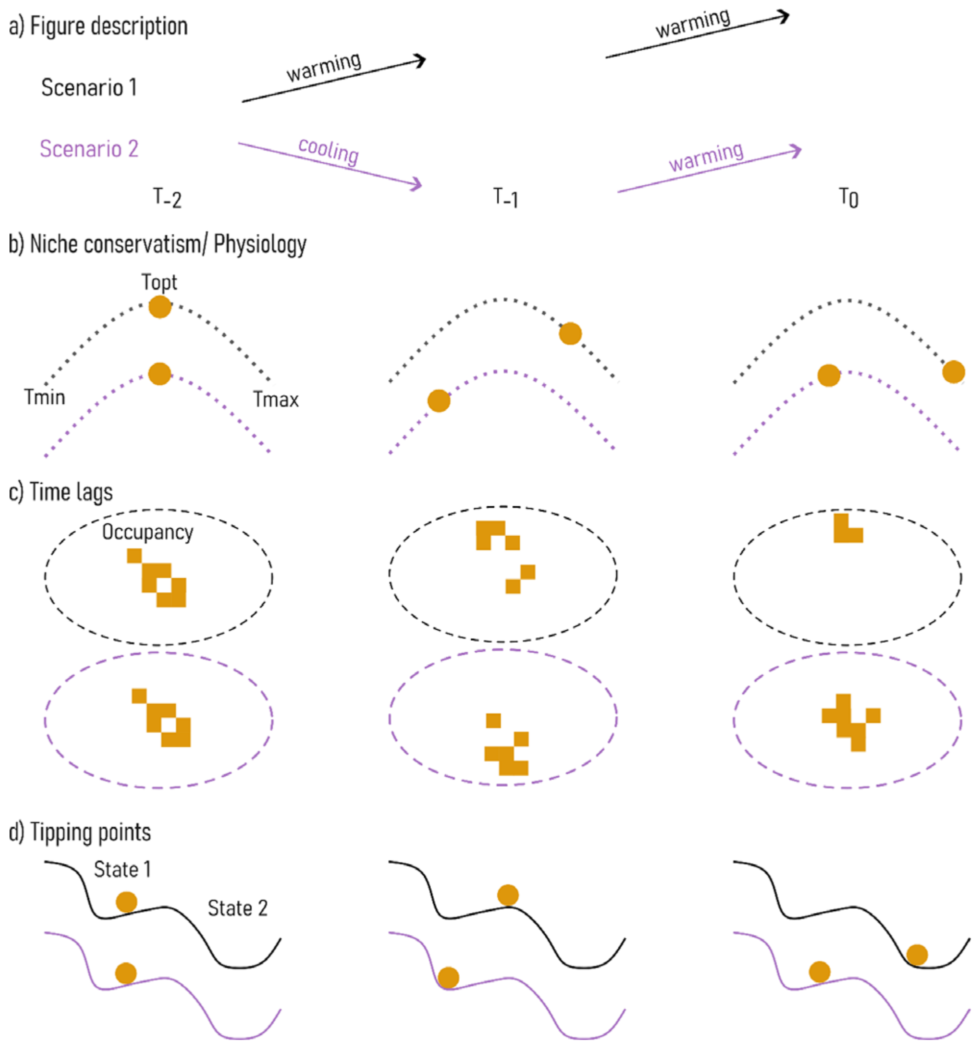


**Figure 3.** The main ecological processes through which climate legacies can affect extinction risk, based on the examined literature (see main text for further discussion). (a) Depicted are two scenarios of climate change over time. Scenario 1 first shows a warming trend from time period $T_{-2}$ to $T_{-1}$, followed by a warming trend from $T_{-1}$ to $T_0$. Contrarily, scenario 2 first shows a cooling trend, followed by the same warming trend as in scenario 1. (b) The effect of the warming trend from $T_{-1}$ to $T_0$ on taxa is mediated by the long-term climatic context, as taxa are forced toward the edges of their adaptation space under scenario 1 while being closer toward their preferences under scenario 2. (c) Time lags such as migration lags might accumulate under scenario 1, resulting in an increased extinction risk. (d) Similarly, critical thresholds within ecosystems might be more easily exceeded under scenario 1.

extinctions can lead to long-lasting legacy effects that determine the susceptibility to extinctions of the remaining species in an ecosystem (Calosi et al., 2019). Nonrandom species loss as a consequence of climate change hereby can either decrease the ability of the remaining species to respond to future climate change (García-Valdés et al., 2018) or buffer the risk of the remaining species (Raffi et al., 1985). Another prominent example of time lag is migration lag, which can impede species from reaching climate refugia (Lunney et al., 2014) and determines dispersal abilities (Yalcin and Leroux, 2018) as well as susceptibility to subsequent climatic changes (Sax et al., 2013; Wiens et al., 2019). Time lags can therefore shape the sensitivity of modern ecosystems to anthropogenic climate changes (Figure 3c).

(iii) Tipping points comprise abrupt shifts within ecosystems (Holling, 1973; Beaugrand, 2015; Lord et al., 2017) and can be caused by climate legacies. The biosphere consists of complex adaptive systems that display multiple alternating states that can shift from one to another abruptly (Solé and Levin, 2022). Exceeding certain temperature thresholds under climate change might trigger unforeseen reinforcing processes and cascading effects that cause significant changes in the Earth system (Friedlingstein et al., 2001; Ren and Leslie, 2011; Song et al., 2021). Crossing critical thresholds could hereby cause ecosystems to switch from one state to another (Beaugrand, 2015; Rocha et al., 2015). While identifying the exact mechanisms causing such changes is challenging, it is undisputed that past climate, and hence climate legacies, strongly influences whether ecosystems reach critical thresholds (Ogle et al., 2015). For example, if a period of warming adds to a previous period of warming, ecological systems are more likely to reach a trigger point for major system changes than if the warming just reverses a previous cooling (Mathes et al., 2021). Similarly, climate change-driven extinctions can affect ecosystem (García-Valdés et al., 2018) or population functioning (Souther and McGraw, 2014) more than random extinctions, with the remaining community being more susceptible to future climatic changes and potential cascading


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dynamics. Tipping points and cascading effects arising from climate legacies are therefore key factors of extinction risk in both past and modern ecosystems (Figure 3d).

## Temporal scale

Our review has shown that climate legacies play out over various temporal scales, ranging from days to millions of years (Figure 2). Although time lags and, in particular, migration lags are likely to dominate over timescales of hundreds to a few thousand years (Urban et al., 2012; Keith et al., 2014; García-Valdés et al., 2018), niche conservatism may be more important on longer timescales covering millions of years (Mayhew et al., 2008; Zhang et al., 2018; Petryshyn et al., 2020; Mathes et al., 2021), even though dispersal limitations can also act over these coarser timescales (Graham, 1999). Physiological thresholds, on the contrary, may lead to severe climate legacies over seasons to years (Griebeler and Gottschalk, 2000; Imperio et al., 2013; Sax et al., 2013; Lunney et al., 2014; Yalcin and Leroux, 2018; Riquelme et al., 2020). Over these finer temporal scales, climate legacies probably do not directly determine extinctions but rather affect population dynamics that can potentially scale up to extinctions, such as community composition, juvenile recruitment or dispersal abilities. As such, climate legacies can determine small-scale population losses over finer temporal scales, and cumulative outcomes eventually lead to global extinctions (e.g., Wiens, 2016). However, it is crucial to note that climate legacies operate across multiple timescales, and the temporal scale examined in any given study depends on the focus of the research and the specific dynamics of the system. It is likely that factors such as species' life history traits, ecological interactions and environmental context can influence the duration and magnitude of climate legacies in shaping extinction dynamics. For example, extinction dynamics over the past 485 million years were found to be not fully explainable without considering the magnitude of climate change in addition to other physiological and taxonomic trait predictors (Malanoski et al., 2024). In addition, ecological processes can act on multiple temporal scales, from which both coarse and fine timescale legacy patterns can emerge (Ogle et al., 2015). A comprehensive understanding of the temporal scale requires careful consideration of these factors in the research design and interpretation of results.

## Methodological approaches

Our review demonstrates that various methods exist to quantify climate legacies. One approach uses regression analysis to evaluate the effect of preceding climate as a predictor for contemporary population dynamics (Imperio et al., 2013; Butler et al., 2017). Similarly, in a continuous time framework, extinction risk at time point $i$ can be regressed against climate conditions from earlier points – such as $i–1$, $i–2$, …, $i–k$ – to capture potential lag effects (Griebeler and Gottschalk, 2000; Mayhew et al., 2008; Saltré et al., 2016). This lagged analysis allows to identify how past climate conditions influence extinction risk over specific time intervals, helping clarify the temporal scale at which climate legacies exert their effects. Instead of using preceding climate in isolation, the interactive effects between preceding and contemporary climate can be determined using regression analysis (Mathes et al., 2021), allowing to quantify how the response of species or populations to contemporary climate changes is mediated by these preceding climate changes. Finally, grouping species into different ecotypes and quantifying how these ecotypes respond to climatic changes (Varela et al., 2015) allows to assess how climate legacies might vary by ecological niche, shedding light on whether certain climate-related adaptions are determining extinction selectivity. To facilitate the application of these approaches, we have developed an R vignette that demonstrates how each of these methods can be implemented (Supplementary Material). This vignette uses the openly available data from the seven studies that quantified climate legacies and reproduces their results with a commented R code. Additionally, to model legacy effects explicitly in ecological analyses, a recent Bayesian stochastic antecedent model offers an innovative approach to capturing multiscale processes and quantifying the length, temporal pattern and strength of legacy effects (Ogle et al., 2015). This model is implemented in OpenBUGS, a free software package for conducting Bayesian statistical analyses. The commented source code can be found in Appendix S2 of Ogle et al. (2015).

## Escalatory dynamics

Climate legacy effects seem to be particularly impactful when concurrent climate changes add to preceding changes in the same direction (Sax et al., 2013; Wiens et al., 2019; Mathes et al., 2021), increasing the probability of shifting into novel climate settings with predominantly negative effects on ecosystems (Figure 3). For example, a short-term warming adding to a preceding warming might be sufficient to push species toward their niche edges (Mathes et al., 2021), potentially surpassing critical thresholds for survival or reproduction. However, the same short-term warming event may have less pronounced impacts if it occurs after a period of cooling, as species may have more resilience to adapt to incremental changes in environmental conditions or as species experience conditions that they or their immediate ancestors have previously experienced. Time lags in ecosystem responses may be extended when contemporary climate change aligns with longer-term trends, intensifying the lagged effects of antecedent conditions on ecological dynamics. High climate velocities might cause species to develop narrower ranges (Araújo and Pearson, 2005; Svenning and Skov, 2007; Svenning et al., 2008) and disturbed rear-edge population dynamics (Hampe and Petit, 2005), which could render those species more susceptible to future warming (Enquist et al., 2019). Similarly, the likelihood of tipping points being surpassed may increase as ecosystems approach critical thresholds due to sustained climate trends, potentially triggering abrupt and irreversible shifts in ecological states (Armstrong McKay et al., 2022).

This is particularly alarming in the context of anthropogenic climate warming, where we observe and predict an accelerating warming trend (Smith et al., 2015; Steffen et al., 2015). As ecosystems experience sustained changes in temperature, precipitation patterns and other climatic variables, the probability of shifting into novel climate spaces will increase with each increment of warming, further magnifying the impact of antecedent conditions on contemporary ecological processes. Contrarily, anthropogenic warming follows a long-term cooling trend over the last 21,000 years (Otto-Bliesner et al., 2006), potentially resulting in less pronounced impacts (Figure 3, Scenario 2). Therefore, identifying the temporal scale relevant for the current biodiversity crisis is crucial. The ability to detect and attribute climate legacy effects accurately, however, may depend not only on the temporal scale of observation but also on the underlying threshold dynamics within ecological systems, highlighting the importance of considering internal ecological


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processes and traits in assessing the long-term consequences of climate change (Malanoski et al., 2024).

## Future perspectives

As our review has shown, only a few studies on the relationship between extinction dynamics and climate included climate legacies (Figure 2), but those that did mostly found large legacy impacts. These impacts were present across a wide range of temporal scales and ecological processes. Individually, these processes are well-known and studied (Svenning et al., 2015), but a solid understanding of their interactions and feedbacks is still lacking (Ogle et al., 2015). Mitigation and conservation efforts under anthropogenic climate change rely heavily on correct predictions of future extinction dynamics, which can only be achieved by acknowledging the effect of the past and by accounting for climate legacy effects.

Scientific progress usually works through examining the patterns in nature and then developing theories that help assimilate observations. Legacy effects cannot be observed directly because antecedent conditions and dependencies are not visible for the bystander. This might be the reason why climate legacy effects are rarely included in ecological studies. Disciplines working on the ecological past with access to observational data over longer time steps, such as historical ecology and palaeontology, may help fill this information gap by identifying and quantifying prevalent climate legacy effects. Furthermore, quantifying climate legacies over deep time and across various temporal scales presents inherent challenges and biases that should be carefully considered. For instance, proxy records – used extensively in paleoclimatic reconstructions – vary significantly in reliability across geologic time (Bennington and Aronson, 2012), and these differences can introduce uncertainty when trying to infer past climate conditions and ecological responses (Hannisdal and Liow, 2018). Moreover, the accuracy of climate models used to estimate species-specific spatiotemporal legacies is also limited (Hawkins and Sutton, 2009; Wiens et al., 2009); these models carry inherent biases due to assumptions made during model construction, such as the relevant spatial resolution (Haerter et al., 2011), which may obscure or alter interpretations of climate legacy effects. Efforts to improve the precision of proxy data and refine model assumptions are therefore crucial to enhance our understanding how these legacies impact extinction dynamics, particularly across the deep-time scales relevant to evolutionary and macroecological studies.

As such, there is an urgent need for analytical frameworks capable of quantifying the effects of climate legacies across scales, such as stochastic antecedent models (Ogle et al., 2015), which offer a promising way to assess these complex interactions. Equally important is the development of open, accessible and user-friendly software to make these analytical tools available to a broader research community. Such tools would facilitate the quantification of climate legacies and encourage more researchers to incorporate these effects into their studies.

While our review highlights the substantial influence of climate legacies on extinction risk, we recognize that most studies to date have focused on limited legacy variables, often examining climate change metrics or climate trends within specific time bins. To fully assess the impact of climate legacies, it is essential to compare their effects against a broader set of extinction predictors (see e.g., Malanoski et al., 2024). For instance, incorporating physiological traits, geographic range size and ecological niche parameters alongside climate legacy variables in extinction models could provide a clearer picture of their relative importance. Moreover, climate legacy effects may interact with these other predictors, amplifying or moderating their influence on extinction risk. Exploring such interactions would help clarify whether and how past climate conditions modify the vulnerability of species in conjunction with other extinction determinants. Developing models that incorporate both the relative and interactive effects of climate legacies and established predictors would thus provide a more comprehensive understanding of extinction dynamics and support more nuanced conservation strategies.

## Conclusions

Climate legacies describe the dependence of contemporary biodiversity dynamics on past climates. Our systematic literature review shows that climate legacies affect species adaptations, population dynamics and juvenile recruitment, determining the extinction risk of species and resilience capacities of ecosystems. Climate legacies arise from ecological processes such as niche conservatism, physiological thresholds, time lags, cascading effects and their interactions. These processes seem to have predominantly negative effects on species and ecosystems when concurrent climate changes add to preceding changes in the same direction, increasing the probability of shifting into novel climate settings. However, few studies quantitatively assess the impact of climate legacies on extinction dynamics in the existing literature, highlighting a research gap. Studies that do quantify climate legacies mostly report substantial impacts. This observed high effect of climate legacy on extinction dynamics suggests important implications for both contemporary ecological research and assessments of extinction risk under future climate change. We emphasize that individual climate-driven events and perturbations to ecosystems cannot be fully understood without considering the climatic context in which these events are embedded. If climate legacies are not incorporated, studies might underestimate or even misinterpret the impact of climatic changes on ecosystems. We therefore hope that the findings reported here, showing that climate legacy effects are prevalent in ecological systems but understudied, instigate more research on climate legacies and a higher integration of legacy effects in future (palaeo-)ecological studies.

**Open peer review.** To view the open peer review materials for this article, please visit http://doi.org/10.1017/ext.2025.2.

**Supplementary material.** The supplementary material for this article can be found at http://doi.org/10.1017/ext.2025.2.

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