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# A unifying framework for studying and managing climate-driven rates of ecological change

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During the Anthropocene and other eras of rapidly changing climates, rates of change of ecological systems can be described as fast, slow or abrupt. Fast ecological responses closely track climate change, slow responses substantively lag climate forcing, causing disequilibria and reduced fitness, and abrupt responses are characterized by nonlinear, threshold-type responses at rates that are large relative to background variability and forcing. All three kinds of climate-driven ecological dynamics are well documented in contemporary studies, palaeoecology and invasion biology. This fast–slow–abrupt conceptual framework helps unify a bifurcated climate-change literature, which tends to separately consider the ecological risks posed by slow or abrupt ecological dynamics. Given the prospect of ongoing climate change for the next several decades to centuries of the Anthropocene and wide variations in ecological rates of change, the theory and practice of managing ecological systems should shift attention from target states to target rates. A rates-focused framework broadens the strategic menu for managers to include options to both slow and accelerate ecological rates of change, seeks to reduce mismatch among climate and ecological rates of change, and provides a unified conceptual framework for tackling the distinct risks associated with fast, slow and abrupt ecological rates of change.

The defining characteristic of the Anthropocene is the pervasive and accelerating rates of change across all components of the Earth system and its interlinked social, physical and ecological subsystems[1–3]. From a geological perspective, the Anthropocene is perhaps best akin to a transitory perturbation, such as the Palaeocene–Eocene Thermal Maximum and other hypsithermals[4], in which the Earth system is responding to a cascading series of anthropogenic forcings that are growing in kind, scope and intensity. Ultimately, the Earth will establish a new post-Anthropocene system state, $10^3$ to $10^4$ years after all geological reservoirs of organic carbon are depleted or tabooed[5–7]. However, from a human perspective, we are now tasked with managing an Earth that is changing rapidly, at rates of change unprecedented in most of human history, at timescales spanning several human generations, towards system states without historical precedent[8].

Hence, the theory and practice of managing ecological systems in the fast-changing Anthropocene should shift from a focus on managing desired states to one focused on managing ongoing rates of change. Traditional conceptual frameworks for managing ecological systems, such as restoration or resilience, often carry implicit assumptions of stable baseline states and goals of restoring ecological systems to historic or pre-baseline states. These frameworks are being discarded, in favour of new, more open-ended approaches such as ecosystem renovation, rewilding and directed and autonomous management strategies[9–13]. Here, we suggest that biospheric management strategies can be distilled to the challenge of jointly managing environmental and eco–evolutionary rates of change[14]. We must reduce or mitigate rates of damaging climate and ecological change, increase rates of eco–evolutionary adaptation and minimize the risk of catastrophic abrupt ecological change.

Given high rates of climate change, three distinct kinds of climate-driven ecological dynamics are possible: fast, slow and abrupt (Box 1). In fast responses (Box figure, panel **a**), species respond quickly and approximately linearly to climate change, thereby maintaining a dynamic equilibrium with their environment[3,15], in ways adaptive for the species concerned, but with negative or positive ripple effects on other ecological system components. In slow responses (Box figure, panel **b**), rates of change in ecological systems are substantively slower than their environmental forcing, leading to ecological disequilibrium[16,17] or debt[18,19], thereby lowering evolutionary fitness as mismatch increases between organisms' optimal and actual environments[20–22]. In abrupt responses (Box figure, panels **c,d**), ecological systems respond rapidly and often unexpectedly to environmental forcing[23–25], due to a variety of nonlinear mechanisms[26–30], with transformative and perhaps catastrophic consequences[31].

However, analyses of the ecological risks posed by climate change have fragmented into at least two distinct sub-literatures: one emphasizing the risks posed by slow ecological responses, disequilibrium and debt[18,32], and the other focusing on abrupt change, regime shifts, tipping points and tipping elements[26,27,31,33]. This bifurcation creates strategic confusion and conflicting guidance, because each risk, when considered alone, incompletely informs decisions about appropriate climate adaptation strategies.

We first establish a unified conceptual framework for understanding and managing climate-driven ecological rates of change by defining and distinguishing fast, slow and abrupt ecological change (Box 1). We then demonstrate strong evidence for each, via a synthetic literature review that focuses primarily but not exclusively on macro-scale species- to community-level vegetation dynamics. This synthesis draws upon a broad range of studies of contemporary climate-driven species range shifts and community dynamics, past climate-driven dynamics and their legacies, and the expansion of non-native species into new regions. This review spans a wide range of timescales, while centring on timescales of 50–200 years[17], because over the twenty-first century management

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**Box 1 | Fast, slow or abrupt ecological dynamics**

The categorization of climate-driven ecological dynamics as fast, slow or abrupt follows standard system theory of assessing the rate of response variables in a system relative to rates of external forcing to that system (Box figure). This framework presupposes for convenience a one-way forcing from climate to ecosystems and ignores, for example, biogeochemical and biogeophysical vegetation–atmosphere feedbacks[175].

The delineation of fast versus slow responses is usually based on linear models of system dynamics. The expected rate of change of an ecological system can be simply modelled as governed by a tracking function, a resistance function, and the current system state relative to historical and potential equilibrial states (see box 2 in ref. [16]):

$$\frac{dE}{dt} = C_T\left(E_{Eq} - E_t\right) - C_R\left(E_t - E_{Hist}\right) \qquad (1)$$

In this framework, the rate of tracking ($dE/dt$) is governed by the difference between the current ecosystem state and its expected equilibrial state given the current climate at time $t$ ($E_{Eq} - E_t$) and a time constant $C_T$ with units of $1/t$. Similarly, rate of resistance is governed by the difference between the current ecological system state and the historical state prior to the onset of climate change ($E_t - E_{Hist}$) and a time constant $C_R$, also with units of $1/t$, that governs rate of resistance. Both $C_T$ and $C_R$ must be equal to or greater than zero, while $dE/dt$ can be positive, zero or negative, depending on the sign of $E_{Eq} - E_t$ and $E_t - E_{Hist}$. Fast ecological systems will have large $C_T$ and small $C_R$ and can quickly track climate change, causing them to be in dynamic equilibrium with their climate forcing[15,16]. Slow systems will have a small $C_T$ or large $C_R$ and large lags between climate forcing and ecological response[15,16]. Not all ecological systems may have a resistance process, which leads to a simpler variant of Eq. (1)[15]:

$$\frac{dE}{dt} = C_T\left(E_{Eq} - E_t\right) \qquad (2)$$

If rates of climate change are low, then $E_{Eq} \approx E_t \approx E_{Hist}$, and rates of ecological change are expected to be low, with little difference in rate between fast- and slow-responding systems. Conversely, if rates of climate change are high, then expected ecological rates of change will be high, due to the resultant offset between the current and equilibrial states of the ecological system ($|E_{Eq} - E_t| >> 0$). Moreover, when rates of climate change are high, the rate differential between 'slow' and 'fast' ecological systems will increase, leading to easier discrimination of fast versus slow dynamics but also higher risk of reduced ecological fitness and other negative impacts caused by mismatch among ecological rates of change. Because both climatic and eco–evolutionary processes operate across timescales of seconds to millions of years[88,176–179], ecological systems can exhibit fast responses at some timescales and be disequilibrial at others.

Abrupt ecological responses can be defined in various ways, including rates of change in an ecological system that are fast relative to typical rates of change in that system[23,25], fast relative to the adaptive capacity of socioecological systems[180], or fast relative to the rate of climate forcing[25,125,181]. Many kinds of stochastic and deterministic mathematical models produce abrupt ecological changes[30,182,183]. Potential driving mechanisms include nonlinear but reversible thresholds in ecological response functions[184], hysteretic systems with alternative stable states[27,185], and strong positive ecosystem–climate feedbacks[186,187]. This multiplicity of mechanisms challenges attribution of causes to observed abrupt changes[23] and also efforts to develop early-warning indicators of abrupt change in real-world systems[146]. To our knowledge, there is no unified mathematical framework that seeks to jointly model fast, slow and abrupt dynamics in an ecological system responding to changing climates. This is an area of needed future work.
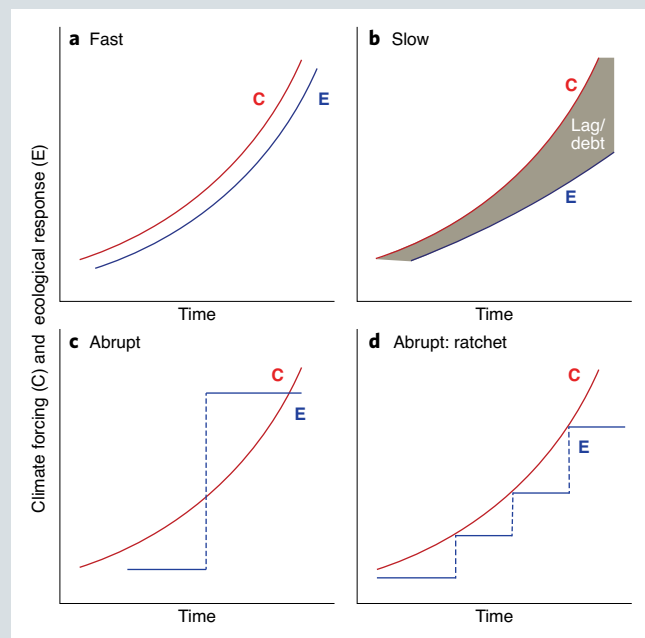


**Conceptual diagram of climate-driven ecological dynamics as fast, slow or abrupt. a**, In fast responses, the rates of climate forcing (C) and ecological response (E) are similar, so that ecological systems quickly adjust to changing environments and responses to recent warming are already detectable. **b**, In slow responses, ecological rates of response lag far behind rates of climatic forcing, creating disequilibrial systems in which mismatches increase among species, evolutionary fitness is lowered and extinction debts accumulate. **c,d**, Abrupt responses are characterized by nonlinear, threshold or hysteretic responses of ecological systems to environmental forcing, as a single event (**c**) or a ratchet of successive abrupt changes (**d**).

decisions will be complicated by the ecological legacies of recent climate changes, the expected further intensification of these climate changes over the coming decades, and the wide range of relevant ecological processes and timescales (Fig. 1). Shifting from state-centred to rates-centred approaches for ecological management carries several major advantages: a more realistic foundation for proactive and pragmatic management in an ever-changing Anthropocene, a broader strategic menu of options to slow or accelerate ecological rates of change, and a unified framework for

understanding and addressing the distinct risks posed by fast, slow and abrupt ecological change.

## Fast climate-driven ecological dynamics

Multiple lines of evidence support fast responses of species abundances and communities to changing climates at timescales of years to decades. These include the study of contemporary species range shifts and community dynamics, high-resolution palaeoecological records of past community dynamics, and the introduction and
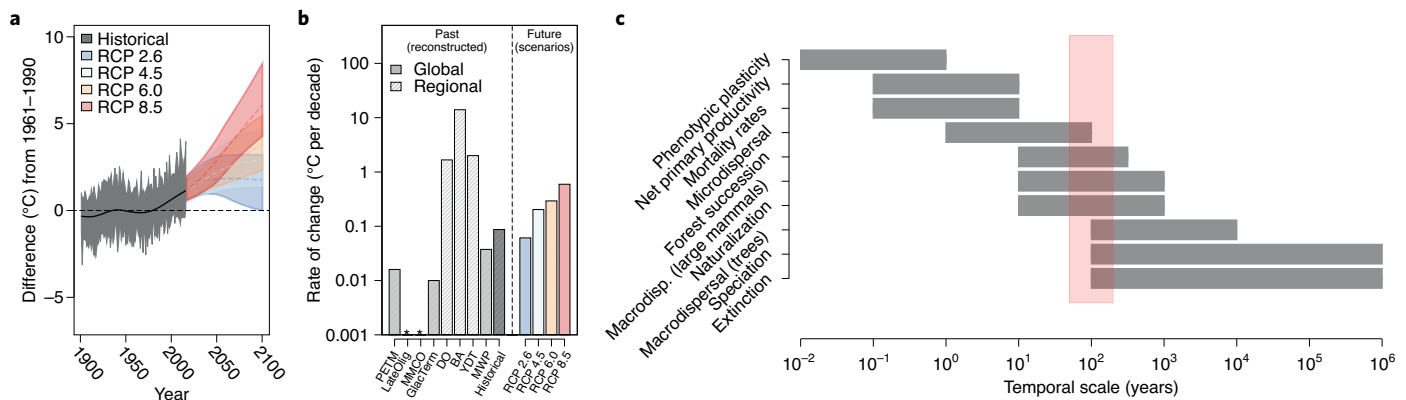
**Fig. 1 | Past, present and future temperature changes and the temporal scale of biological responses. a–c**, Historic and projected global temperature trends for AD 1900 to 2100 (**a**), rates of projected and past temperature change (**b**) and timescale of biological responses (**c**). In **a**, historical temperatures (AD 1900–2013)[171] are shown as anomalies (solid black line) relative to AD 1961–1990 global means (dotted black line at y = 0) and annual variability (grey shading). Projections for AD 2013–2100 are based on 19 Coupled Model Intercomparison Project Phase 5 (CMIP5) simulations[172] and are shown as temperature anomalies (coloured dashed lines) and inter-model variability (coloured shading). RCP, Representative Concentration Pathway; PETM, Palaeocene–Eocene Thermal Maximum (56 million years ago (Ma)); LateOlig, Late Oligocene warming (26 Ma); MMCO, Mid-Miocene Climatic Optimum (14.8 Ma); GlacTerm, glacial terminations (nine terminations over the past 800 kyr); DO, Dansgaard–Oeschger events (20 events between 10 and 80 thousand years ago (ka)); BA, Bølling-Allerød warming (14.7 ka); YDT, Younger Dryas Termination (11.7 ka); MWP, Medieval Warm Period (AD 500 to 1000). See Supplementary Table 1 for estimated rates of projected and past temperature change and sources. Past rates of change shown in **b** primarily represent global mean annual surface temperature changes, but for millennial-scale climate variations (DO, BA and YDT), estimates represent rates of change in the North Atlantic and adjacent regions; this change in spatial extent is indicated by cross-hatching. Asterisks indicate rates of change that are too slow to be shown in this plotting. Rates of ecological processes shown in **c** are drawn from reviews of the literature on rates of change and timescales of processes[17,88,173,174], with the vertical red bar showing the focal timescale of 50–200 years. As rates of warming accelerate, ecological dynamics are increasingly dominated by differential timescales of ecological response within and among species.

expansion of non-native species into new environments. These studies suggest several rules of thumb about the processes and characteristics of ecological systems, including human intervention, that enable fast ecological responses (Fig. 2).

Ecological systems are responding now to the sustained anthropogenic warming underway since at least the 1970s[34], with detectable changes in, for example, species ranges and composition[3,35], phenology[36,37] and vegetation productivity[38] that all appear to be fast responses to recent temperature rises. Marine species ranges are moving poleward at average rates of 72 km per decade[35]. Plant species ranges are moving at rates of 17.6 ± 2.9 km per decade northwards and 11 ± 1.8 m per decade upslope[39]. In the Alps, the upslope rate of plant range centroids in mature forests is 29.4 ± 10.9 m per decade[40]. Increases in Alpine plant species richness have closely tracked twentieth- and twenty-first-century warming, with no discernible local time lag[3]. Cultivar tree species transplanted poleward of their historic ranges are establishing self-reproducing unmanaged populations[41]. Rates of community turnover have increased during the last century, across a wide range of biomes and taxa[42,43]. The timing of phenological events in the Northern Hemisphere is shifting by 2.8 days per decade[44]. Avian populations significantly decline in abundance and richness after individual heatwaves, indicating high sensitivity and fast responses to thermal environment[45].

Determining whether observed ecological trends truly represent fast responses to climate change can be difficult, because ecological systems respond to many anthropogenic factors[46,47]. 'Fast' versus 'slow' responses are easiest to detect when rates of climate change are high, because the rate differential between fast- and slow-responding ecological systems will be highest. However, species respond to multiple climate variables, each changing at different rates and directions[48], which can challenge determination of whether an ecological response is fast or slow. Studies that rely only upon temperature indices tend to underestimate expected rates of ecological change[49] and the individualism of climate-driven species-level dynamics[50].

Good examples of fast ecological dynamics come from high-resolution palaeoecological and palaeoclimatic records, because many past climate events were abrupt even by contemporary standards (Fig. 1b)[14,51,52], enough time has elapsed for ecological responses to emerge fully, and attribution to climate forcing is simplified by a smaller human footprint. Rates of temperature and climate change during the last deglaciation in Greenland and regions around the North Atlantic were remarkable (Fig. 1b), with, for example, 9–14 °C warming in Greenland in 1–3 years at the start of the Bølling period, approximately 14,700 years ago[53,54], and 8–12 °C warming in Greenland and 3 °C warming within a few years to decades in northern Europe at the start of the Holocene, 11,700 years ago[53,54].

The large vegetation changes observed during the last deglaciation are hypothesized to have been caused by a combination of fast and slow (next section) ecological responses, with fast local changes in species abundances and community turnover (years to decades) and, for many species, slower migrational responses (centuries to millennia). Much of the complex individualistic species and community dynamics observed during the last deglaciation can be explained as fast responses to multidimensional climate change, combined with unique Hutchinsonian species niches[15,55]. This hypothesis is supported by early species distribution models, in which climatic response surfaces were used to predict past climates and the distributions of other species, with high predictive success[56]. Continental-scale maps of fossil-pollen distributions in Europe indicate distribution shifts at least 4 to 10 km per decade[57], while in eastern North America, biotic velocities were as fast as climate velocities, at the mapped resolution of 500 to 1,000 years[58]. For high-resolution and well-dated fossil pollen records that are co-located with independent palaeoclimatic proxies, the lag between rapid temperature forcing and initial changes in local plant abundances is often <100 years[59] and as short as 0 to 20 years[60]. The wide use of micropalaeontological data to infer past climates relies on the assumption of dynamic equilibrium between species abundances
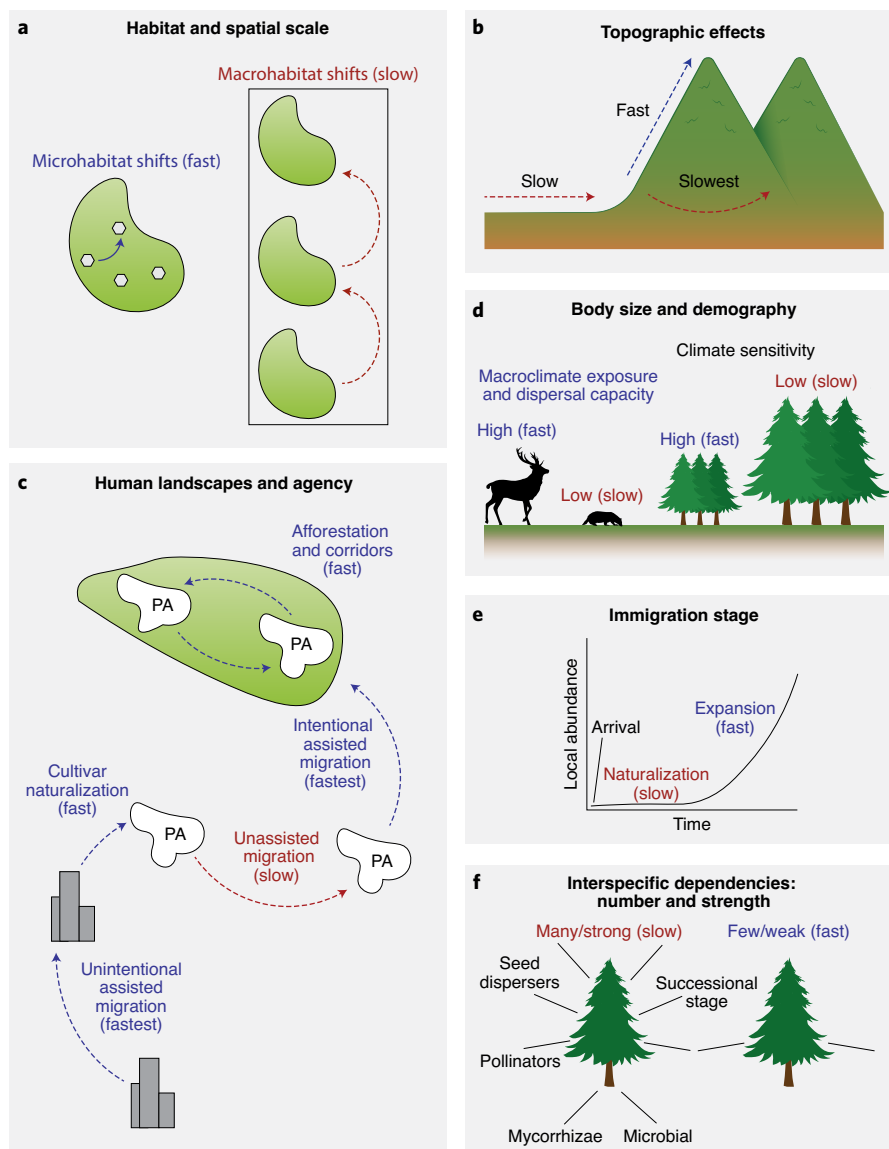
**Fig. 2 | Processes governing the ecological timescales of response to climate change. a–f,** Variations in the timescale of response to climate change within and across ecological systems depend on various geographic, ecological and anthropogenic factors; for example, microhabitat versus macrohabitat shifts (**a**), topographic effects (**b**), human landscapes and agency (**c**), demography and body size (**d**), immigration stage (**e**) and the number and strength of interspecific interactions and dependencies (**f**). Blue text and arrows indicate processes that promote fast ecological responses to climate change, whereas red text and arrows indicate processes that promote slow or disequilibrial responses. PA, protected area.

and their environment at the relevant timescale[15,61]. Aquatic and terrestrial communities show similarly fast annual- to decadal-scale changes in species abundance and community turnover to rapid climate forcing, irrespective of organismal lifespan, although immigration was delayed by centuries for some tree species[62,63]. Eco–evolutionary models also predict that changes in abundance are faster than changes in range[64], consistent with the fossil record.

In invasion biology, species with large ranges, high dispersal capacity and broad climate niches in their native ranges can fill unaided their climate niches in new continents on a timescale of a few decades[65,66]. In population biology, juveniles are often the most sensitive to environmental fluctuations[67], allowing fast population responses to environmental change through quick shifts in rates of juvenile recruitment and mortality[68–70]. Climate-driven mortality rates can be accelerated by intensified disturbance regimes[71] and amplified by biotic feedbacks; for example, pest or pathogen outbreaks[72] or collapse of mutualistic relationships[73].

From these contemporary, palaeoecological and invasion-biology studies, several useful rules of thumb emerge about the processes enabling fast ecological dynamics (Fig. 2). First, high topographic and habitat heterogeneity enables fast ecological adaptation by placing various microclimates in close proximity, enabling species to quickly move among nearby microclimates (Fig. 2a), or, in mountainous regions, move upslope (Fig. 2b). Much of the best evidence for fast distributional responses comes from mountains[3,40,74]. Second, demography affects climate sensitivity and response time (Fig. 2d), with juveniles often more susceptible to climate extreme events[68]. Third, body size also matters; among plants, woody trees may be more sensitive to macroclimate variation, whereas herbaceous plants may be more sensitive to microclimates and more able to persist in local microrefugia despite large macroclimatic changes[75]. Similarly, among terrestrial vertebrates, larger animals may be more exposed to macroclimate variations and have higher dispersal capability, enabling fast

responses[76]. Fourth, species with fewer dependencies on facilitative interactions may be able to respond more quickly than species with more obligate interactions (Fig. 2f)[77].

Fifth, human agency, whether intentional or accidental, can vastly increase rates of ecological responses to climate change (Fig. 2c). Naturalistic reforestation and corridors facilitate the movement of species among microhabitats and protected areas. Managed relocation (also known as assisted migration or assisted colonization) of at-risk species can accelerate adaptive range shifts by species[78,79]. Cultivars in nurseries often are $10^2$–$10^3$ km north of their historic range limit[80], with cultivars in gardens often now establishing self-reproducing populations outside their historic range. *Magnolia tripetala* is now growing in New England forests, well north of its historic northern range limit, following horticultural introduction in the nineteenth century[41]. In Europe, *Castanea sativa*, *Juglans regia* and other tree species have all established naturalized populations north of their historic ranges[81].

## Slow dynamics, disequilibria, debt and mismatch

Conversely, because many ecological processes operate at timescales slower than current rates of climate forcing, many species and ecosystems are now in climatic disequilibrium. The evolutionary fitness of individual species decreases as mismatch increases between their optimal environments and those that they occupy[22]. Related concepts include climate debt[18,32]; tolerance niches[82], in which species temporarily persist in climates outside their fundamental niche; evolutionary or extinction debt, in which biodiversity losses caused by climate change accrue long afterwards[83,84]; and phenological or camouflage mismatch[36,85–87]. Slow dynamics and time lags can result from multiple processes, including dispersal limitation and barriers to dispersal (Fig. 2a,b,d); persistence of adult individuals in regions that have become unfavourable to recruitment and juveniles; delays to successful colonization and establishment caused by Allee effects, small population sizes and poor local adaptation, and priority effects (Fig. 2e); high dependencies on other species (Fig. 2f), and little or no human facilitation (Fig. 2c).

The growing fields of disequilibrial and temporal ecology study transient community dynamics in non-stationary environments[16,88,89]. In disequilibrial dynamics, a central parameter is the time lag (or response time) between climate forcing and ecological response[15,16]. Eco–evolutionary models predict that extinction debts can persist for hundreds of years after climate forcing[84]. Controlled climate experiments show that herbaceous community responses can accumulate for many years after treatment onset[90]. In Andean plant communities, rates of temperature-driven compositional responses are ten times lower than temperature trends[91].

Disequilibrial lags can be assessed spatially, by measuring the distance between current species distributions and those predicted by current climates. For example, bird populations shifted northwards 91 km between 1989 and 2006, but temperature zones moved 273 km, implying a spatial lag of 182 km (ref. [32]). Metapopulation models fitted to tree distributions in eastern North America suggest that many major species are in climatic disequilibrium, particularly at northern range limits[92], consistent with analyses of adult and juvenile tree distributions that indicate no evidence that tree ranges are shifting northward[93]. In France, lowland plant populations in low-relief areas had the largest climate debts[19,94]. Comparisons of the climatic distributions of native and naturalized populations can also support climate disequilibrium[17,95]. For example, of 51 native and naturalized species in Europe and the United States, 22 had naturalized populations living beyond their native climate niches[96], suggesting that the native populations are in climatic disequilibrium. A global comparison of native and naturalized pine populations suggested that climate disequilibrium is pervasive in native populations and that species with small ranges and narrow niches are more likely to be in climate disequilibrium[97]. Mismatches between the observed

climates for a region and those inferred given the species present and assumptions of stable community–climate relationships can indicate disequilibrium[16,98,99]. However, all such spatial diagnostics of disequilibrium face the challenges of attribution mentioned in the previous section: ecological systems respond to many abiotic, biotic and anthropogenic factors, making it difficult sometimes to confidently attribute differences in, for example, native and naturalized distributions to climate disequilibrium.

The palaeoecological record provides clear evidence of local extinction debt and lagged range shifts at timescales of centuries to millennia. In the western United States, after the end-Pleistocene warming, extinction debts played out over thousands of years, with the most cold-adapted taxa going locally extinct first and more cool-adapted taxa later[100]. On St. Paul Island, a population of woolly mammoths persisted on a postage stamp of an island (~100 km$^2$) for 8,000 years before going extinct, possibly due to hydroclimate variability[101]. In eastern North America and Europe, many tree species expanded their ranges through the Holocene, thousands of years after the largest temperature rises. *Fagus grandifolia* continued to expand its range in the northern Great Lakes throughout the Holocene, moving around the barriers posed by Lake Michigan[102], reaching its historic northwestern range limit approximately 2,500 to 1,500 years ago[103], where it may still have an unfilled climate niche[104]. Similarly, the arrival of *Betula pubescens* in western Norway lagged warming by ~450 years (ref. [105]) and the immigration of *Pinus* across the Alps lagged warming by ~800 years[106]. The current distribution of European tree diversity is partially predicted by full-glacial climates or distances to glacial refugia, suggesting that many European tree species have unfilled climate niches[81,107]. Glacial–interglacial climate velocity predicts contemporary biodiversity and endemism at the species level[108] and at higher phylogenetic levels[109], suggesting that small-ranged taxa are either still in disequilibrium with interglacial climates or adapting via microhabitat switching.

Studies of species invasions show that after introduction, an exotic species frequently does not instantaneously colonize (that is, establish self-perpetuating populations) or become naturalized, that is, become widely incorporated within the resident flora[110]. During the naturalization phase, range dynamics are often characterized by slow rates of range expansion and niche infilling[111]. The lag between introduction and naturalization can last 3 to 50 years (refs. [112,113]). This lag period is widely recognized[111,113–116]. In marine species, more recently introduced species have smaller ranges than earlier introductions[117]. Likewise, recently introduced plants in Australia[118,119] and Chile[115,120] show either no range expansion or slow rates of infilling.

Differential rates of change among components of ecological systems lead to mismatches that can reduce fitness for individual species[36,121], cause transient novel communities to emerge[122] and alter ecological function[86]. Phenological mismatches to abiotic factors can reduce fitness by, for example, causing flowering to occur at suboptimal temperatures[85], increasing damage due to late-spring frosts[123], or via camouflage mismatches[20]. Phenological mismatches among species can disrupt trophic interactions[121,124] and alter ecosystem functioning[86].

## Abrupt responses

Many ecological systems are susceptible to changing abruptly[23,125,126], at scales from local to global[26], with some abrupt changes clearly attributable to climate forcing[69,73,127]. Risk of abrupt change is acutest for ecological systems in which the keystone species are long-lived and slow-growing, such as corals and trees, because this broadens the range of timescales operating within these systems and enables them to quickly switch from slow- to fast-operating processes. Iconic examples include the worldwide increase in the frequency and extent of coral beaching events due to heat stress imposed by rising ocean temperatures and El Niño–Southern Oscillation (ENSO)
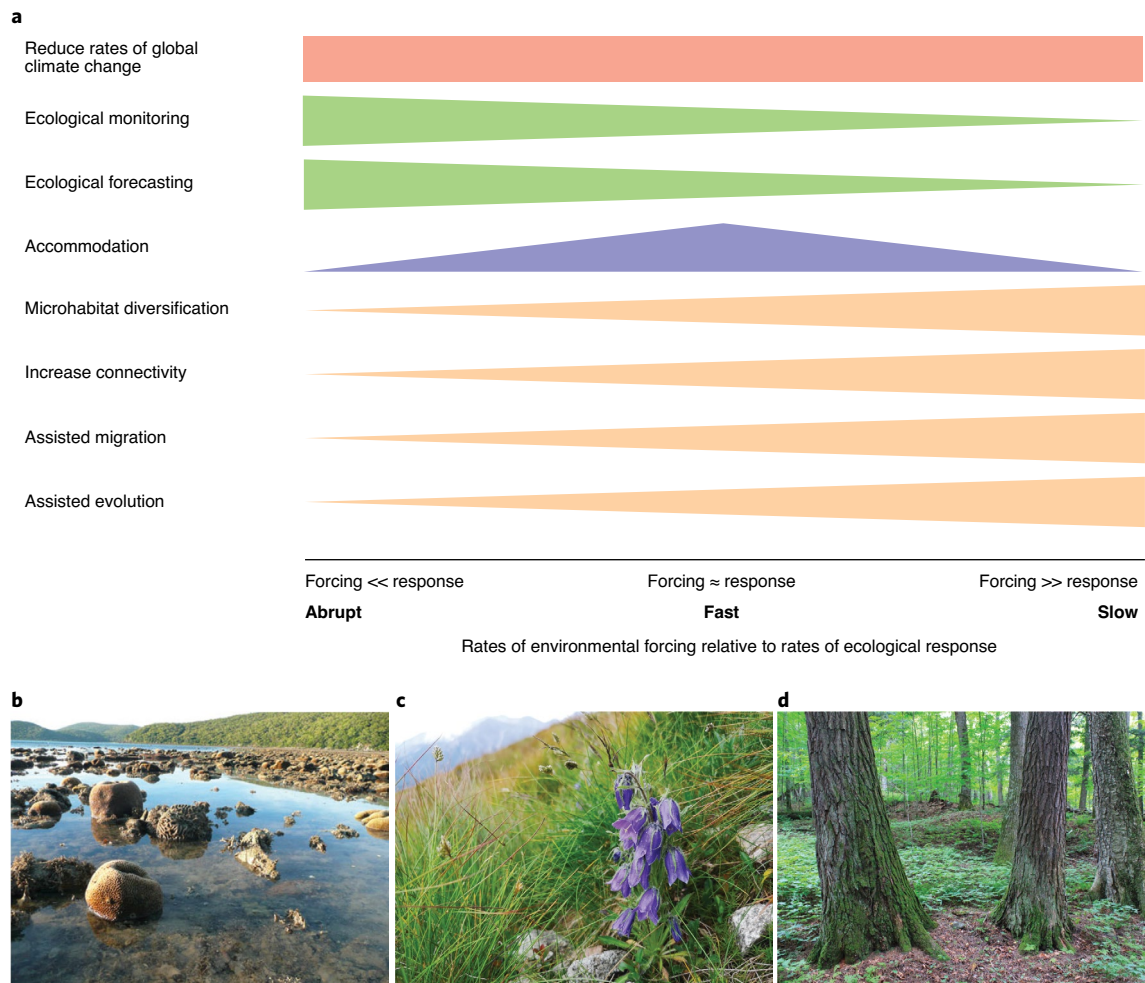
**Fig. 3 | In a rates-based framework for designing management strategies, the key consideration is the rates of climate forcing relative to rates of response in ecological systems. a**, Different mixtures of strategies will be appropriate for systems characterized by abrupt, fast or slow ecological dynamics. **b–d**, Illustrative examples of ecosystems characterized by abrupt, fast or slow responses to rising temperatures: shallow-water coral ecosystems, which are collapsing due to increased adult mortality and recruitment failures with heat stress (**b**); alpine ecosystems, where elevational range shifts are currently underway (**c**); and multi-centennial to millennial range expansions of temperate trees after post-glacial warming (**d**). Credit: ARC Center of Excellence for Coral Reef Studies (**b**); Jens-Christian Svenning (**c**); Stephen T. Jackson, Southwest Climate Adaptation Science Center, US Geological Survey (**d**).

variability[24,69] and the increases in tree mortality and decreased regeneration in western North America, linked to droughts, pest outbreaks and intensified fire regime[70–72].

During the Holocene, abrupt changes in ecological systems were common and often attributable to hydroclimate variability or shifts in disturbance regime[25,128]. In eastern North America, the range-wide collapse of *Tsuga canadensis*, occurring at some sites in <10 years (ref. [129]), is linked to North Atlantic climate variability and regional drought[128], although intrinsic processes may have contributed[130]. In the Galapagos, diatom and mangrove communities experienced both extrinsic and intrinsic regime shifts[131]. Plant range expansions may operate by a ratchet mechanism, characterized by abrupt range expansions interspersed with stability[68]. In the western United States, *Pinus edulis* and *Juniperus osteosperma* experienced intervals of range stability lasting thousands of years, interspersed with decadal-scale episodes of range expansion, paced by hydroclimate variability[81,132–136].

Systems known to have multiple stable states are at high risk of abrupt change. Sharp discontinuities in ecological gradients can suggest alternate stable states separated by thresholds[137,138], as do spatial mosaics[126,127] or temporal mosaics[25]. In the tropics, fire, large herbivores, and vegetation feedbacks produce multiple stable states among forests, savannas and grasslands[139]. In the boreal forest, multiple tipping points may exist among multiple system states[28]. Abrupt changes in ecological systems can be triggered by extreme weather events, fires or other forms of pulse disturbance events that trigger mass mortality[140]. Plants well adapted to brief temperature fluctuations can be damaged by persistent heat waves and drought[141] or experience recruitment failures[142].

Definitive attribution of abrupt ecological change to climate drivers is challenged by the multiplicity of processes, numerical representations of those processes, and varying relevant timescales[23,143]. Nonlinear ecological dynamics can be produced by a wide variety of deterministic and stochastic processes[26–28]. Efforts are underway to identify early warning signals of abrupt change[27,33,144], but predicting the timing of abrupt changes remains challenging[145,146].

## Managing ecological rates in a rapidly changing Anthropocene

Ongoing climate change, combined with other anthropogenic changes, is driving a tectonic shift in the goals, language and conceptual framework underpinning conservation biology and restoration ecology[9,10,147–149]. The field has moved away from goals and concepts rooted in assumptions of stable historic baselines[149,150] and towards

concepts of active ecosystem renovation[10], rewilding[151] and novel ecosystems[152–154]. This shift has stirred debate[155,156]. However, despite extensive conversations about proper terminology and target state, rates of change usually are addressed only implicitly or in passing[149,157].

Shifting attention from states to rates is usefully clarifying. First, it clarifies that, for the next several decades to centuries, there will be no steady states anywhere in the surface Earth system, as greenhouse gas concentrations rise. Hence, target ecosystem states are useful, but more immediate concerns will usually involve managing ongoing rates of change. Second, a focus on rates encompasses traditional goals of ecosystem restoration (holding rates of change at zero, or reversing undesirable trajectories) while broadening the menu of strategic options to include newer approaches that emphasize accelerating desirable rates of change. These range from ecosystem-level interventions such as rewilding, which promotes the autonomous capacity of ecosystems to dynamically maintain biodiversity[151,158], to species-focused interventions such as assisted migration and managed relocation[79,159] or assisted evolution[160]. Third, because ongoing change in the Earth system is now a given, the critical need is to reduce mismatches among rates of change: between rates of climate change and eco–evolutionary adaptation (large differences leading to, for example, climatic debt, disequilibrium or lowered evolutionary fitness), between species (leading to, for example, phenological mismatch or pollinator failure), and between ecosystem services and societal adaptation. Fourth, some challenges such as phenological mismatch are inherently problems of rate rather than problems of state; they are transient problems caused by differential rates of forcing and response. Fifth, by unifying the fragmented literatures on climate change and ecological risk (slow and disequilibrial versus abrupt and threshold-type dynamics), a rates-centred management approach helps identify strategies that are universally useful versus those particular to fast, slow or abrupt dynamics (Fig. 3).

Reducing rates of global climate change is a universal solution. Reducing rates buys time for species to adapt and reduces risk of pushing ecological systems past tipping points[31]. Species display a high adaptive capacity for past temperature rises, as long as rates are not too fast[161] or are synergistic with other extinction drivers[4]. Therefore, climate-mitigation strategies that flatten the curve towards slower rates of change are well aligned with the available science and support pragmatic optimism. There is a victory in every kg of carbon not emitted.

For ecological systems characterized by fast responses to climate change, optimal management strategies can be minimalist, emphasizing accommodation[9], mitigation of undesired secondary outcomes, and monitoring (Fig. 3). For ecological systems prone to abrupt change, with damaging ecological and economic consequences, better forecasting ability is needed, powered by high-quality, open-data ecological monitoring networks[162,163], closely integrated with better forecasting models[164–166]. This approach has steadily improved the predictive skill and time horizon of meteorological forecasting[167].

For systems characterized by slow responses, the key goal is to reduce rate mismatch, by slowing rates of climate change or accelerating rates of eco–evolutionary adaptation. Climate change can be slowed both globally and locally, by enhancing countervailing microclimate trends; for example, by increasing shade in stream environments[168]. Multiple levers exist to increase rates of eco–evolutionary adaptation (Figs. 2 and 3); for example, increase local microclimate and habitat diversity to facilitate microhabitat switching[169], increase habitat connectivity, or increase rates of dispersal and colonization for dispersal-limited species of concern[159]. Resistance strategies that slow undesirable rates of ecological change[9,147] are possible but may require increasingly high levels of intervention and resources as climate change proceeds. From a rates perspective, a realistic goal for most resistance strategies is rarely ecosystem stabilization, but rather managed retreats; slowing rather than halting rates of undesired change.

The study and management of ecological systems responding to climate change is challenged by the interactions among processes, each operating at different timescales[23,170] and across multiple levels of ecological organization. A further challenge is that management activities often operate at narrower timescales (sub-annual to sub-decadal) than the climate-driven ecological dynamics reviewed here. Usually, within a single system, managers will need to simultaneously accelerate some rates of change and slow others. For example, a manager might simultaneously seek to both facilitate leading-edge range expansions of dispersal-limited species and slow trailing-edge population extirpations. In a temperate forested landscape with a heterogeneous land-use history and species composition, a manager might pursue different strategies for different forest stands, preserving in one place an old-growth forest stand, while elsewhere introducing seedlings of species that are likely to flourish in the projected climates of the coming decades. As always in ecological systems, the particular mixtures of management strategies will need to be customized to the characteristics of the systems being managed.

In summary, ecological rates of change can be fast, slow or abrupt relative to climatic drivers. All three are well documented, each poses different risks, and each suggests different suites of management interventions (Fig. 3). An integrated awareness of fast, slow and abrupt dynamics adds complexity to the study and management of ecological systems, because of the multiplicity of these interacting processes and the difficulty of predicting emergent outcomes. Nonetheless, a focus on managing rates of change provides the conceptual foundation for proactive and pragmatic optimism, because ecological systems have demonstrated a high adaptive capacity to past temperature variations. Humans have the ability to speed up and slow down rates of ecological response, both intentionally and accidentally (Fig. 2c). We can flatten the curve of climate change and increase both the rates of eco–evolutionary adaptation and our own rates of learning, forecasting and adaptation.

## References

1. Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O. & Ludwig, C. The trajectory of the Anthropocene: The Great Acceleration. *Anthr. Rev.* **2**, 81–98 (2015).
2. Steffen, W., Grinevald, J., Crutzen, P. & McNeill, J. The Anthropocene: conceptual and historical perspectives. *Phil. Trans. R. Soc. A* **369**, 842–867 (2011).
3. Steinbauer, M. J. et al. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* **556**, 231–234 (2018).
4. McInerney, F. A. & Wing, S. L. 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 (2011).
5. Herrero, C., García-Olivares, A. & Pelegrí, J. L. Impact of anthropogenic $CO_2$ on the next glacial cycle. *Clim. Change* **122**, 283–298 (2014).
6. Clark, P. U. et al. Consequences of twenty-first-century policy for multi-millennial climate and sea-level change. *Nat. Clim. Change* **6**, 360–369 (2016).
7. Berger, A. & Loutre, M. F. An exceptionally long interglacial ahead? *Science* **297**, 1287–1288 (2002).
8. Burke, K. D. et al. Pliocene and Eocene provide best analogues for near-future climates. *Proc. Natl Acad. Sci. USA* **115**, 13288–13293 (2018).
9. Fisichelli, N. A., Schuurman, G. W. & Hoffman, C. H. Is 'resilience' maladaptive? Towards an accurate lexicon for climate change adaptation. *Environ. Manag.* **57**, 753–758 (2016).
10. Prober, S. M., Doerr, V. A. J., Broadhurst, L. M., Williams, K. J. & Dickson, F. Shifting the conservation paradigm: a synthesis of options for renovating nature under climate change. *Ecol. Monogr.* **89**, e01333 (2019).
11. Scheffers, B. R. & Pecl, G. Persecuting, protecting or ignoring biodiversity under climate change. *Nat. Clim. Change* **9**, 581–586 (2019).
12. Barnosky, A. D. et al. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* **355**, eaah4787 (2017).
13. Hughes, F. M. R., Adams, W. M. & Stroh, P. A. When is open-endedness desirable in restoration projects? *Restor. Ecol.* **20**, 291–295 (2012).
14. Williams, J. W. & Burke, K. in *Climate Change and Biodiversity: Transforming the Biosphere* (eds Lovejoy, T & Hannah, L.) 128–141 (Yale Univ. Press, 2019).

15. Webb, T. III. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* **67**, 75–91 (1986).

16. Blonder, B. et al. Predictability in community dynamics. *Ecol. Lett.* **20**, 293–306 (2017).

17. Svenning, J.-C. & Sandel, B. Disequilibrium vegetation dynamics under future climate change. *Am. J. Bot.* **100**, 1266–1286 (2013).

18. Huntley, B. et al. Climatic disequilibrium threatens conservation priority forests. *Conserv. Lett.* **11**, e12349 (2018).

19. Bertrand, R. et al. Ecological constraints increase the climatic debt in forests. *Nat. Commun.* **7**, 12643 (2016).

20. Zimova, M., Mills, L. S. & Nowak, J. J. High fitness costs of climate change-induced camouflage mismatch. *Ecol. Lett.* **19**, 299–307 (2016).

21. Visser, M. E. & Gienapp, P. Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* **3**, 879–885 (2019).

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

23. Ratajczak, Z. et al. Abrupt change in ecological systems: inference and diagnosis. *Trends Ecol. Evol.* **33**, 513–526 (2018).

24. Hughes, T. P. et al. Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373–377 (2017).

25. Williams, J. W., Blois, J. L. & Shuman, B. N. Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. *J. Ecol.* **99**, 664–677 (2011).

26. Lenton, T. M. et al. Tipping elements in the Earth's climate system. *Proc. Natl Acad. Sci. USA* **105**, 1786–1793 (2008).

27. Scheffer, M. et al. Anticipating critical transitions. *Science* **338**, 344–348 (2012).

28. Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E. H. & Chapin, F. S. Thresholds for boreal biome transitions. *Proc. Natl Acad. Sci. USA* **109**, 21384–21389 (2012).

29. Boettiger, C. & Hastings, A. Tipping points: from patterns to predictions. *Nature* **493**, 157–158 (2013).

30. Boettiger, C., Ross, N. & Hastings, A. Early warning signals: the charted and uncharted territories. *Theor. Ecol.* **6**, 255–264 (2013).

31. Lenton, T. M. et al. Climate tipping points — too risky to bet against. *Nature* **575**, 593–595 (2019).

32. Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. Birds are tracking climate warming, but not fast enough. *Proc. R. Soc. B* **275**, 2743–2748 (2008).

33. Dakos, V., Carpenter, S. R., van Nes, E. H. & Scheffer, M. Resilience indicators: prospects and limitations for early warnings of regime shifts. *Phil. Trans. R. Soc. B* **370**, 20130263 (2014).

34. IPCC in *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. et al.) Summary for Policymakers (Cambridge Univ. Press, 2013).

35. Pecl, G. T. et al. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* **355**, eaai9214 (2017).

36. Kudo, G. & Ida, T. Y. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* **94**, 2311–2320 (2013).

37. Körner, C. & Basler, D. Phenology under global warming. *Science* **327**, 1461–1462 (2010).

38. Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D. & Willis, K. J. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* **531**, 229–232 (2016).

39. Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011).

40. Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P. & Brisse, H. A significant upward shift in plant species optimum elevation during the 20th Century. *Science* **320**, 1768–1771 (2008).

41. Bellemare, J. & Deeg, C. Horticultural escape and naturalization of Magnolia tripetala in western Massachusetts: biogeographic context and possible relationship to recent climate change. *Rhodora* **117**, 371–383 (2015).

42. Blowes, S. A. et al. The geography of biodiversity change in marine and terrestrial assemblages. *Science* **366**, 339–345 (2019).

43. Dornelas, M. et al. Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**, 296–299 (2014).

44. Parmesan, C. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Change Biol.* **13**, 1860–1872 (2007).

45. Albright, T. P. et al. Heat waves measured with MODIS land surface temperature data predict changes in avian community structure. *Remote Sens. Environ.* **115**, 245–254 (2011).

46. Cazelles, K. et al. Homogenization of freshwater lakes: recent compositional shifts in fish communities are explained by gamefish movement and not climate change. *Glob. Change Biol.* **25**, 4222–4233 (2019).

47. Guo, F., Lenoir, J. & Bonebrake, T. C. Land-use change interacts with climate to determine elevational species redistribution. *Nat. Commun.* **9**, 1315 (2018).

48. Abatzoglou, J. T., Dobrowski, S. Z. & Parks, S. A. Multivariate climate departures have outpaced univariate changes across global lands. *Sci. Rep.* **10**, 3891 (2020).

49. VanDerWal, J. et al. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nat. Clim. Change* **3**, 239–243 (2013).

50. Ordonez, A., Williams, J. W. & Svenning, J. C. Mapping climatic mechanisms likely to favour the emergence of novel communities. *Nat. Clim. Change* **6**, 1104–1109 (2016).

51. Hof, C., Levinsky, I., Araújo, M. B. & Rahbek, C. Rethinking species' ability to cope with rapid climate change. *Glob. Change Biol.* **17**, 2987–2990 (2011).

52. Brown, S. C., Wigley, T. M. L., Otto-Bliesner, B. L., Rahbek, C. & Fordham, D. A. Persistent Quaternary climate refugia are hospices for biodiversity in the Anthropocene. *Nat. Clim. Change* **10**, 244–248 (2020).

53. Buizert, C. et al. Greenland temperature response to climate forcing during the last deglaciation. *Science* **345**, 1177–1180 (2014).

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

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

56. Prentice, I. C., Bartlein, P. J. & Webb, T. III. Vegetation and climate change in eastern North America since the last glacial maximum. *Ecology* **72**, 2038–2056 (1991).

57. Giesecke, T., Brewer, S., Finsinger, W., Leydet, M. & Bradshaw, R. H. W. Patterns and dynamics of European vegetation change over the last 15,000 years. *J. Biogeogr.* **44**, 1441–1456 (2017).

58. Ordonez, A. & Williams, J. W. Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecol. Lett.* **16**, 773–781 (2013).

59. Williams, J. W., Post, D. M., Cwynar, L. C., Lotter, A. F. & Levesque, A. J. Rapid and widespread vegetation responses to past climate change in the North Atlantic region. *Geology* **30**, 971–974 (2002).

60. Tinner, W. & Lotter, A. F. Central European vegetation response to abrupt climate change at 8.2 ka. *Geology* **29**, 551–554 (2001).

61. Juggins, S. Quantitative reconstructions in paleolimnology: new paradigm or sick science? *Quat. Sci. Rev.* **64**, 20–32 (2013).

62. Ammann, B. et al. Responses to rapid warming at Termination 1a at Gerzensee (Central Europe): primary succession, albedo, soils, lake development, and ecological interactions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **391**, 111–131 (2013).

63. Ammann, B., von Grafenstein, U. & van Raden, U. J. Biotic responses to rapid warming about 14,685 yr BP: introduction to a case study at Gerzensee (Switzerland). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **391**, 3–12 (2013).

64. Cotto, O. et al. A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nat. Commun.* **8**, 15399 (2017).

65. Petitpierre, B. et al. Climatic niche shifts are rare among terrestrial plant invaders. *Science* **335**, 1344–1348 (2012).

66. Hui, C., Roura-Pascual, N., Brotons, L., Robinson, R. A. & Evans, K. L. Flexible dispersal strategies in native and non-native ranges: environmental quality and the 'good–stay, bad–disperse' rule. *Ecography* **35**, 1024–1032 (2012).

67. Grubb, P. J. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* **52**, 107–145 (1977).

68. Jackson, S. T., Betancourt, J. L., Booth, R. K. & Gray, S. T. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proc. Natl Acad. Sci. USA* **106**, 19685–19692 (2009).

69. Hughes, T. P. et al. Global warming impairs stock–recruitment dynamics of corals. *Nature* **568**, 387–390 (2019).

70. Stevens-Rumann, C. S. et al. Evidence for declining forest resilience to wildfires under climate change. *Ecol. Lett.* **21**, 243–252 (2018).

71. Keeley, J. E., van Mantgem, P. & Falk, D. A. Fire, climate and changing forests. *Nat. Plants* **5**, 774–775 (2019).

72. Raffa, K. F., Powell, E. N. & Townsend, P. A. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proc. Natl Acad. Sci. USA* **110**, 2193–2198 (2013).

73. Hughes, T. P. et al. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* **359**, 80–83 (2018).

74. Feeley, K. J. et al. Upslope migration of Andean trees. *J. Biogeogr.* **38**, 783–791 (2011).

75. Ricklefs, R. E. & Latham, R. E. Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *Am. Nat.* **139**, 1305–1321 (1992).

76. McCain, C. M. & King, S. R. B. Body size and activity times mediate mammalian responses to climate change. *Glob. Change Biol.* **20**, 1760–1769 (2014).

77. Pither, J., Pickles, B. J., Simard, S. W., Ordonez, A. & Williams, J. W. Below-ground biotic interactions moderated the postglacial range dynamics of trees. *New Phytol.* **220**, 1148–1160 (2018).

78. Lawler, J. J. & Olden, J. D. Reframing the debate over assisted colonization. *Front. Ecol. Environ.* **9**, 569–574 (2011).

79. Schwartz, M. W. et al. Managed relocation: integrating the scientific, regulatory, and ethical challenges. *BioScience* **62**, 732–743 (2012).

80. Van der Veken, S., Hermy, M., Vellend, M., Knapen, A. & Verheyen, K. Garden plants get a head start on climate change. *Front. Ecol. Environ.* **6**, 212–216 (2008).

81. Svenning, J.-C. & Skov, F. Limited filling of the potential range in European tree species. *Ecol. Lett.* **7**, 565–573 (2004).

82. Sax, D. F., Early, R. & Bellemare, J. Niche syndromes, species extinction risks, and management under climate change. *Trends Ecol. Evol.* **28**, 517–523 (2013).

83. Kuussaari, M. et al. Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* **24**, 564–571 (2009).

84. Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A. & Loeuille, N. Eco-evolutionary responses of biodiversity to climate change. *Nat. Clim. Change* **2**, 747–751 (2012).

85. Wheeler, H. C., Høye, T. T., Schmidt, N. M., Svenning, J.-C. & Forchhammer, M. C. Phenological mismatch with abiotic conditions—implications for flowering in Arctic plants. *Ecology* **96**, 775–787 (2015).

86. Beard, K. H., Kelsey, K. C., Leffler, A. J. & Welker, J. M. The missing angle: ecosystem consequences of phenological mismatch. *Trends Ecol. Evol.* **34**, 885–888 (2019).

87. Chamberlain, C. J., Cook, B. I., de Cortazar Atauri, I. G. & Wolkovich, E. M. Rethinking false spring risk. *Glob. Change Biol.* **25**, 2209–2220 (2019).

88. Wolkovich, E. M., Cook, B. I., McLauchlan, K. K. & Davies, T. J. Temporal ecology in the Anthropocene. *Ecol. Lett.* **17**, 1365–1379 (2014).

89. Pagel, J. et al. Mismatches between demographic niches and geographic distributions are strongest in poorly dispersed and highly persistent plant species. *Proc. Natl Acad. Sci. USA* **117**, 3663–3669 (2020).

90. Komatsu, K. J. et al. Global change effects on plant communities are magnified by time and the number of global change factors imposed. *Proc. Natl Acad. Sci. USA* **116**, 17867–17873 (2019).

91. Fadrique, B. et al. Widespread but heterogeneous responses of Andean forests to climate change. *Nature* **564**, 207–212 (2018).

92. Talluto, M. V., Boulangeat, I., Vissault, S., Thuiller, W. & Gravel, D. Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nat. Ecol. Evol.* **1**, 0182 (2017).

93. Zhu, K., Woodall, C. W. & Clark, J. S. Failure to migrate: lack of tree range expansion in response to climate change. *Glob. Change Biol.* **18**, 1042–1052 (2012).

94. Bertrand, R. et al. Changes in plant community composition lag behind climate warming in lowland forests. *Nature* **479**, 517–520 (2011).

95. Bocsi, T. et al. Plants' native distributions do not reflect climatic tolerance. *Divers. Distrib.* **22**, 615–624 (2016).

96. Early, R. & Sax, D. F. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Glob. Ecol. Biogeogr.* **23**, 1356–1365 (2014).

97. Perret, D. L., Leslie, A. B. & Sax, D. F. Naturalized distributions show that climatic disequilibrium is structured by niche size in pines (*Pinus* L.). *Glob. Ecol. Biogeogr.* **28**, 429–441 (2019).

98. Blonder, B. et al. Linking environmental filtering and disequilibrium to biogeography with a community climate framework. *Ecology* **96**, 972–985 (2015).

99. Knight, C. A. et al. Community assembly and climate mismatch in Late-Quaternary eastern North American pollen assemblages. *Am. Nat.* **195**, 166–180 (2020).

100. Butterfield, B. J., Anderson, R. S., Holmgren, C. A. & Betancourt, J. L. Extinction debt and delayed colonization have had comparable but unique effects on plant community–climate lags since the Last Glacial Maximum. *Glob. Ecol. Biogeogr.* **28**, 1067–1077 (2019).

101. Graham, R. W. et al. Timing and causes of a middle Holocene mammoth extinction on St. Paul Island, Alaska. *Proc. Natl Acad. Sci. USA* **113**, 9310–9314 (2016).

102. Woods, K. D. & Davis, M. B. Paleoecology of range limits: beech in the Upper Peninsula of Michigan. *Ecology* **70**, 681–696 (1989).

103. Jackson, S. T. et al. Inferring local to regional changes in forest composition from Holocene macrofossils and pollen of a small lake in central Upper Michigan. *Quat. Sci. Rev.* **98**, 60–73 (2014).

104. Seeley, M., Goring, S. & Williams, J. W. Testing hypotheses about environmental and dispersal controls on *Fagus grandifolia* distributions in the upper Midwest Great Lakes region. *J. Biogeogr.* **46**, 405–419 (2019).

105. Birks, H. J. B. & Birks, H. H. Biological responses to rapid climate change at the Younger Dryas—Holocene transition at Kråkenes, western Norway. *Holocene* **18**, 19–30 (2008).

106. Ammann, B. et al. Vegetation responses to rapid warming and to minor climatic fluctuations during the Late-Glacial Interstadial (GI-1) at Gerzensee (Switzerland). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **391**, 40–59 (2013).

107. Svenning, J.-C. & Skov, F. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecol. Lett.* **10**, 453–460 (2007).

108. Sandel, B. et al. The influence of late Quaternary climate-change velocity on species endemism. *Science* **334**, 660–664 (2011).

109. Feng, G. et al. Species and phylogenetic endemism in angiosperm trees across the Northern Hemisphere are jointly shaped by modern climate and glacial–interglacial climate change. *Glob. Ecol. Biogeogr.* **28**, 1393–1402 (2019).

110. Richardson, D. M. et al. Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.* **6**, 93–107 (2000).

111. Sakai, A. K. et al. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **32**, 305–332 (2001).

112. Hui, C. & Richardson, D. M. *Invasion Dynamics* (Oxford Univ. Press, 2017).

113. Kowarik, I. in *Plant Invasions. General Aspects and Special Problems* (eds Pysek, P. et al.) 15–39 (SPB Academic Publishing, 1995).

114. Bruce, K. A., Cameron, G. N. & Harcombe, P. A. Initiation of a new woodland type on the Texas Coastal Prairie by the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.). *Bull. Torrey Bot. Club* **122**, 215–225 (1995).

115. Castro, S. A., Figueroa, J. A., Muñoz-Schick, M. & Jaksic, F. M. Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile. *Divers. Distrib.* **11**, 183–191 (2005).

116. Hoffmann, J. H. & Moran, V. C. The invasive weed *Sesbania punicea* in South Africa and prospects for its biological control. *S. Afr. J. Sci.* **84**, 740–472 (1988).

117. Byers, J. E. et al. Invasion expansion: time since introduction best predicts global ranges of marine invaders. *Sci. Rep.* **5**, 12436 (2015).

118. Phillips, M. L., Murray, B. R., Leishman, M. R. & Ingram, R. The naturalization to invasion transition: are there introduction-history correlates of invasiveness in exotic plants of Australia? *Austral Ecol.* **35**, 695–703 (2010).

119. Scott, J. K. & Panetta, F. D. Predicting the Australian weed status of southern African plants. *J. Biogeogr.* **20**, 87–93 (1993).

120. Arroyo, M. T. K., Rozzi, R., Simonetti, J. A., Marquet, P. & Sallaberry, M. in *Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecosystems* (eds Mittermeier, R. A. et al.) 161–171 (Cemex, Conservation International, 1999).

121. Zarnetske, P. L., Skelly, D. K. & Urban, M. C. Biotic multipliers of climate change. *Science* **336**, 1516–1518 (2012).

122. Ordonez, A. & Williams, J. W. Projected climate reshuffling based on multivariate climate-availability, climate-analog, and climate-velocity analyses: implications for community disaggregation. *Clim. Change* **119**, 659–675 (2013).

123. Zohner, C. M. et al. Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. *Proc. Natl Acad. Sci. USA* **117**, 12192–12200 (2020).

124. Renner, S. S. & Zohner, C. M. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annu. Rev. Ecol. Evol. Syst.* **49**, 165–182 (2018).

125. Turner, M. G. et al. Climate change, ecosystems, and abrupt change: science priorities. *Phil. Trans. R. Soc. B* **375**, 20190105 (2020).

126. Rietkerk, M., Dekker, S. C., de Ruiter, P. C. & van de Koppel, J. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* **305**, 1926–1929 (2004).

127. Calder, W. J. & Shuman, B. N. Extensive wildfires, climate change, and an abrupt state change in subalpine ribbon forests, Colorado. *Ecology* **98**, 2585–2600 (2017).

128. Shuman, B. N., Marsicek, J., Oswald, W. W. & Foster, D. R. Predictable hydrological and ecological responses to Holocene North Atlantic variability. *Proc. Natl Acad. Sci. USA* **116**, 5985–5990 (2019).

129. Allison, T. D., Moeller, R. E. & Davis, M. B. Pollen in laminated sediments provides evidence of mid-Holocene forest pathogen outbreak. *Ecology* **67**, 1101–1105 (1986).

130. Ramiadantsoa, T., Stegner, M. A., Williams, J. W. & Ives, A. R. The potential role of intrinsic processes in generating abrupt and quasi-synchronous tree declines during the Holocene. *Ecology* **100**, e02579 (2019).

131. Seddon, A. W. R., Froyd, C. A., Witkowski, A. & Willis, K. J. A quantitative framework for analysis of regime shifts in a Galápagos coastal lagoon. *Ecology* **95**, 3046–3055 (2014).

132. Gray, S. T., Betancourt, J. L., Jackson, S. J. & Eddy, R. G. Role of multidecadal climatic variability in a range extension of pinyon pine. *Ecology* **87**, 1124–1130 (2006).

133. Lyford, M. E., Jackson, S. T., Betancourt, J. L. & Gray, S. T. Influence of landscape structure and climate variability on a late Holocene plant migration. *Ecol. Monogr.* **73**, 567–583 (2003).

134. Tinner, W. & Lotter, A. F. Holocene expansions of *Fagus silvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? *Quat. Sci. Rev.* **25**, 526–549 (2006).

135. Saltré, F. A. et al. Climate or migration: what limited European beech post-glacial colonization? *Glob. Ecol. Biogeogr.* **22**, 1217–1227 (2013).

136. Ruosch, M. et al. Past and future evolution of Abies alba forests in Europe – comparison of a dynamic vegetation model with palaeo data and observations. *Glob. Change Biol.* **22**, 727–740 (2016).

137. Danz, N. P., Frelich, L. E., Reich, P. B. & Niemi, G. J. Do vegetation boundaries display smooth or abrupt spatial transitions along environmental gradients? Evidence from the prairie–forest biome boundary of historic Minnesota, USA. *J. Veg. Sci.* **24**, 1129–1140 (2013).

138. Grimm, E. C. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecol. Monogr.* **54**, 291–311 (1984).

139. Staver, A. C., Archibald, S. & Levin, S. A. The global extent and determinants of savanna and forest as alternative biome states. *Science* **334**, 230–232 (2011).

140. Thomson, J. A. et al. Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Glob. Change Biol.* **21**, 1463–1474 (2015).

141. Teskey, R. et al. Responses of tree species to heat waves and extreme heat events. *Plant Cell Environ.* **38**, 1699–1712 (2015).

142. Hansen, W. D. & Turner, M. G. Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying. *Ecol. Monogr.* **89**, e01340 (2019).

143. Bestelmeyer, B. T. et al. Analysis of abrupt transitions in ecological systems. *Ecosphere* **2**, 129 (2011).

144. Lenton, T. M. Early warning of climate tipping points. *Nat. Clim. Change* **1**, 201–209 (2011).

145. Hastings, A. & Wysham, D. B. Regime shifts in ecological systems can occur with no warning. *Ecol. Lett.* **13**, 464–472 (2010).

146. Boettiger, C. & Hastings, A. Quantifying limits to detection of early warning for critical transitions. *J. R. Soc. Interface* **9**, 2527–2539 (2012).

147. Millar, C. I., Stephenson, N. L. & Stephens, S. L. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* **17**, 2145–2151 (2007).

148. Choi, Y. D. Restoration ecology to the future: a call for new paradigm. *Restor. Ecol.* **15**, 351–353 (2007).

149. Corlett, R. T. Restoration, reintroduction, and rewilding in a changing world. *Trends Ecol. Evol.* **31**, 453–462 (2016).

150. Sprugel, D. G. Disturbance, equilibrium, and environmental variability: what is 'Natural' vegetation in a changing environment? *Biol. Conserv.* **58**, 1–18 (1991).

151. Perino, A. et al. Rewilding complex ecosystems. *Science* **364**, eaav5570 (2019).

152. Jackson, S. T. & Hobbs, R. J. Ecological restoration in the light of ecological history. *Science* **325**, 567–569 (2009).

153. Radeloff, V. C. et al. The rise of novelty in ecosystems. *Ecol. Appl.* **25**, 2051–2068 (2015).

154. Truitt, A. M. et al. What is novel about novel ecosystems: managing change in an ever-changing world. *Environ. Manag.* **55**, 1217–1226 (2015).

155. Murcia, C. et al. A critique of the 'novel ecosystem' concept. *Trends Ecol. Evol.* **29**, 548–553 (2014).

156. Ricciardi, A. & Simberloff, D. Assisted colonization is not a viable conservation strategy. *Trends Ecol. Evol.* **24**, 248–253 (2009).

157. Svenning, J.-C. Proactive conservation and restoration of botanical diversity in the Anthropocene's "rambunctious garden". *Am. J. Bot.* **105**, 963–966 (2018).

158. Jepson, P. Recoverable Earth: a twenty-first century environmental narrative. *Ambio* **48**, 123–130 (2019).

159. Hoegh-Guldberg, O. et al. Assisted colonization and rapid climate change. *Science* **321**, 345–346 (2008).

160. van Oppen, M. J. H., Oliver, J. K., Putnam, H. M. & Gates, R. D. Building coral reef resilience through assisted evolution. *Proc. Natl Acad. Sci. USA* **112**, 2307–2313 (2015).

161. Willis, K. J. & MacDonald, G. M. Long-term ecological records and their relevance to climate change predictions for a warmer world. *Annu. Rev. Ecol. Evol. Syst.* **42**, 267–287 (2011).

162. Farley, S. S., Dawson, A., Goring, S. J. & Williams, J. W. Situating ecology as a big data science: Current advances, challenges, and solutions. *BioScience* **68**, 563–576 (2018).

163. Brown, T. B. et al. Using phenocams to monitor our changing Earth: toward a global phenocam network. *Front. Ecol. Environ.* **14**, 84–93 (2016).

164. Clark, J. S. et al. Ecological forecasts: an emerging imperative. *Science* **293**, 657–660 (2001).

165. Dietze, M. C. et al. Iterative near-term ecological forecasting: needs, opportunities, and challenges. *Proc. Natl Acad. Sci. USA* **115**, 1424–1432 (2018).

166. Dietze, M. C. *Ecological Forecasting* (Princeton Univ. Press, 2017).

167. Bauer, P., Thorpe, A. & Brunet, G. The quiet revolution of numerical weather prediction. *Nature* **525**, 47–55 (2015).

168. Thomas, S. M., Griffiths, S. W. & Ormerod, S. J. Adapting streams for climate change using riparian broadleaf trees and its consequences for stream salmonids. *Freshw. Biol.* **60**, 64–77 (2015).

169. Greenwood, O., Mossman, H. L., Suggitt, A. J., Curtis, R. J. & Maclean, I. M. D. Using *in situ* management to conserve biodiversity under climate change. *J. Appl. Ecol.* **53**, 885–894 (2016).

170. Carpenter, S. R. & Turner, M. G. Hares and tortoises: interactions of fast and slow variables in ecosystems. *Ecosystems* **3**, 495–497 (2000).

171. Harris, I., Jones, P., Osborn, T. & Lister, D. Updated high-resolution grids of monthly climatic observations–the CRU TS3.10 dataset. *Int. J. Climatol.* **34**, 623–642 (2014).

172. Bureau of Reclamation *Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections: Release of Hydrology Projections, Comparison with Preceding Information, and Summary of User Needs* (US Department of the Interior, Bureau of Reclamation, Technical Services Center, 2014).

173. Delcourt, H. R. & Delcourt, P. A. *Quaternary Ecology: A Paleoecological Perspective* (Chapman & Hall, 1991).

174. IPCC in *Climate Change 2014: Impacts, Adaptation, and Vulnerability* (eds Field, C. B. et al.) 1–32 (Cambridge Univ. Press, 2014).

175. Bonan, G. B. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* **320**, 1444–1449 (2008).

176. McDowell, P. F., Webb, T. III & Bartlein, P. J. in *The Earth as Transformed by Human Action* (eds Turner, B. L. II et al.) 143–162 (Cambridge Univ. Press, 1990).

177. Delcourt, P. A. & Delcourt, H. R. *Long-Term Forest Dynamics of the Temperate Zone: A Case Study of Late-Quaternary Forests in Eastern North America* (Springer-Verlag, 1987).

178. Turner, M. G., Dale, V. H. & Gardner, R. H. Predicting across scales: theory development and testing. *Landsc. Ecol.* **3**, 245–252 (1989).

179. Kidwell, S. M. Biology in the Anthropocene: challenges and insights from young fossil records. *Proc. Natl Acad. Sci. USA* **12**, 4922–4929 (2015).

180. National Research Council *Abrupt Climate Change: Inevitable Surprises* (National Academy Press, 2002).

181. Rahmstorf, S. in *Encyclopedia of Ocean Sciences* (eds Steele, J. et al.) 1–6 (Academic Press, 2001).

182. Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. Catastrophic shifts in ecosystems. *Nature* **413**, 591–596 (2001).

183. Staver, A. C., Archibald, S. & Levin, S. Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states. *Ecology* **92**, 1063–1072 (2011).

184. Andersen, T., Carstensen, J., Hernández-Garcia, E. & Duarte, C. M. Ecological thresholds and regime shifts: approaches to identification. *Trends Ecol. Evol.* **24**, 49–57 (2009).

185. Scheffer, M. & Carpenter, S. R. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* **18**, 648–656 (2003).

186. Claussen, M. Late Quaternary vegetation-climate feedbacks. *Clim. Past* **5**, 203–216 (2009).

187. Liu, Z., Notaro, M. & Gallimore, R. Indirect vegetation-soil moisture feedback with application to Holocene North Africa climate. *Glob. Change Biol.* **16**, 1733–1743 (2010).

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## Author contributions

J.W.W., A.O. and J.-C.S. jointly contributed to paper planning and discussion. J.W.W. and A.O. developed figures. J.W.W. led writing with contributions from A.O. and J.-C.S.

## Competing interests

The authors declare no competing interests.

## Additional information

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