Received: 14 January 2025 | Accepted: 12 May 2025

DOI: 10.1111/1365-2435.70079

BRITISH ECOLOGICAL SOCIETY Functional Ecology

REVIEW

Ecological acclimation: A framework to integrate fast and slow responses to climate change

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Funding information
NSF Directorate for Biological Sciences, Grant/Award Number: 204754

Handling Editor: Sarah Elizabeth Diamond

Abstract

1. Ecological responses to climate change occur across vastly different time-scales, from minutes for physiological plasticity to decades or centuries for community turnover and evolutionary adaptation. Accurately predicting the range of ecosystem trajectories will require models that incorporate both fast processes that may keep pace with climate change and slower ones likely to lag behind and generate disequilibrium dynamics. However, the knowledge necessary for this integration is currently fragmented across disciplines.
2. We develop 'ecological acclimation' as a unifying framework to emphasize the similarity of dynamics driven by processes operating on dramatically different time-scales and levels of biological organization. The framework focuses on ecoclimate sensitivities, measured as the change in an ecological response variable per unit of climate change. Acclimation processes acting at different time-scales cause these sensitivities to shift in magnitude and even direction over time.
3. We highlight shifting ecoclimate sensitivities in case studies from diverse ecosystems, including terrestrial plant communities, coral reefs and soil microbiomes.
4. Models predicting future ecosystem states inevitably make assumptions about acclimation processes; these assumptions must be explicit for users to evaluate whether a model is appropriate for a given forecast horizon. Similarly, decision frameworks that clearly account for multiple acclimation processes and their distinct time-scales will help natural resource managers plan for ecological impacts of climate change from years to many decades into the future.

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5. We outline a synthetic research programme focused on the time-scales of ecological acclimation to reduce uncertainty in ecological forecasts.

KEYWORDS
climate adaptation, disequilibrium, ecoclimate sensitivity, forecast horizon, lags, nonstationarity, time-scale, transient dynamics

1 | INTRODUCTION

Climate shapes ecosystem structure and function, and it is changing at a pace that is unprecedented in recent times (IPCC, 2023). Some ecological processes, such as physiological plasticity, changes in behaviour and phenological shifts, are fast enough to generate clear responses to climate variation within organisms' lifetimes (Badeck et al., 2004; Beever et al., 2017; Nicotra et al., 2010). On the other hand, slower responses that operate over many generations, such as evolutionary adaptation and dispersal-limited species range shifts, are likely to lag behind the pace of climate change (Alexander et al., 2018; Block et al., 2022; Wilczek et al., 2014). As a result, short- and long-term ecological responses to a change in climate may differ in magnitude and even direction (Perret et al., 2024; Smith et al., 2009). For example, soil organic carbon in an alpine plant community decreased initially with experimental warming due to a loss of heat-intolerant forbs, but increased after more than two decades of warming as heat-tolerant shrubs with more degradable litter became dominant (Harte et al., 2015). Such changes in ecological responses over time are common but present a challenge: management decisions that are informed by short-term experiments or observations (over several years) may be effective initially but risk becoming counterproductive at the scale of multiple decades and beyond (Hastings, 2016). On the other hand, management actions based on long-term equilibrium expectations (i.e. from space-for-time substitutions) risk failing to anticipate the negative impacts of near-term, transient dynamics (Francis et al., 2021). Effective investments in conservation, restoration and climate adaptation require accurate predictions of the full range of possible ecosystem trajectories and how they will respond to our interventions at time-scales ranging from years to the end of this century and beyond (Lawler, 2009; Lynch, Thompson, et al., 2022).

One barrier to forecasting ecosystem states at decision-relevant time-scales is that knowledge about ecological responses and the rates at which they occur is scattered across subdisciplines. Researchers studying evolutionary adaptation (Crous et al., 2016), community turnover (Avolio et al., 2021), species' distribution shifts (Malone et al., 2018; Pagel & Schurr, 2012), biogeochemical cycles (Kim et al., 2016) and changing disturbance regimes (Krauss & Osland, 2019) often do not consider their combined influence on ecosystems. For example, short-term trait plasticity may slow down long-term evolutionary adaptation by reducing selection pressure (Donelson et al., 2019), but such interactions remain understudied. Additionally, slow processes are difficult to study using traditional experiments and observational studies in real time. Knowledge about the time-scales of processes such as soil development and range expansions of long-lived plants is largely limited to paleoecological records (George et al., 2023; Lang et al., 2023; Raiho et al., 2022) or depends on inference from contemporary biogeographical patterns (Seliger et al., 2021; Svenning et al., 2015). Our poorly integrated understanding of the time-scales of multi-generational ecological responses to climate change and their collective impacts on ecosystem structure and function creates tremendous uncertainty in projections beyond the near-term (Carpenter, 2002; Felton et al., 2022; Luo et al., 2011; Perret et al., 2024). In order to anticipate growing disequilibrium between climate and ecosystems (Svenning & Sandel, 2013), we need a framework to relate the time-scales of change in ecosystem structure and function to the rate of climate change. An important step is adopting a shared vocabulary and approach to focus research on quantifying the time-scales of lagging processes and, ultimately, clarifying and reducing sources of uncertainty in decadal-scale ecological forecasts.

Here, we propose 'ecological acclimation' as a conceptual umbrella to synthesize knowledge across disciplines and highlight the similarity of processes operating at vastly different time-scales (Figure 1). At the core of this framework is the notion that many components of ecosystems adjust over time to reduce mismatch—or disequilibrium—with the current climate. This expectation, though sometimes implicit, forms the foundation for much of ecology (Blonder et al., 2017; Loehle, 2018; Luo et al., 2017; Svenning & Sandel, 2013; Williams et al., 2020). A focus on ecological acclimation emphasizes that ecosystem responses to climate forcing may shift over time in strength and even direction because multiple ecological acclimation processes play out over different time-scales. To account for these time-dependent responses, we borrow terminology from climate science (Williams et al., 2022) and distinguish between an ecosystem's 'initial sensitivity' to climate change, determined primarily by fast processes, and 'equilibrium sensitivity' (Table 1), which emerges after both fast and slow ecological acclimation processes have had time to unfold. In the interim between initial and equilibrium responses, 'transient sensitivities' may fluctuate in magnitude and direction over time. By explicitly recognizing that sensitivities may shift over time, we can explain contrasting short-term and long-term responses to climate drivers in both experiments and observational studies (Figure 2) and show that the relative importance of fast and slow

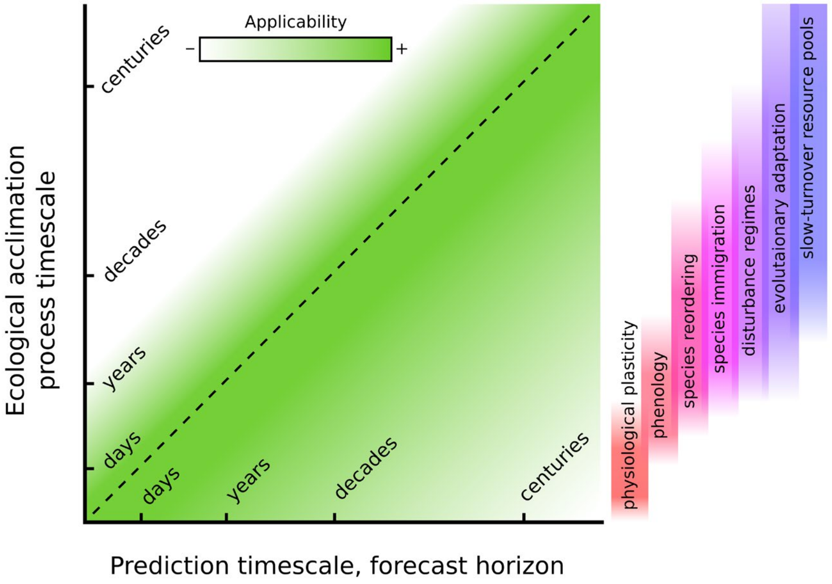

FIGURE 1 The applicability of ecological acclimation processes to predictive models depends on the time-scales of the process and the time-scale, or forecast horizon, of the prediction: when making short-term predictions, primarily fast processes such as plasticity and phenology need to be considered, but long-term predictions should incorporate the dynamics of both slow and fast processes. The bars to the right of the chart show examples of ecological acclimation processes, colour-coded by the time-scale at which they occur, with red representing the faster processes, and blue the slowest. The height and fading gradients of the bars represent variation and uncertainty about the time-scale of the processes. In the chart, darker green represents the time-scales of processes that have the greatest influence on—or applicability for—predictions made at the corresponding time-scales. The dashed line shows the one-to-one relationship.

processes for prediction depends on the length of the forecast horizon (Figure 1; Adler et al., 2020).

The goal of this paper is to provide the conceptual synthesis necessary to enable accurate ecological forecasts across time horizons and to plan for the consequences of ecosystem-climate disequilibrium. This synthesis links physiological acclimation, evolutionary adaptation and community turnover as processes unified by similar dynamics but distinguished by the time-scales at which they operate. We first define key terms to facilitate communication across ecology, evolution, biogeochemistry and climate science. Second, we examine evidence for ecological acclimation in four case studies from terrestrial and marine ecosystems that involve plants, animals and soil microbes. An additional line of evidence comes from discrepancies in measures of ecological sensitivity to variation in climate over time compared to variation across space. Third, we outline recommendations for predictive modelling across time-scales. Fourth, we discuss the implications of the ecological acclimation framework for natural resource management. Finally, we outline future research needed to reduce critical uncertainties about ecological acclimation processes and their time-scales.

2 | DEFINING ECOLOGICAL ACCLIMATION

We propose ‘ecological acclimation’ as a new term for the suite of processes that act to reduce climate disequilibrium over time (Figure 1). Disequilibrium is the difference between the current ecological state and the state expected in the long term given persistence of the current climate. Ecological acclimation processes push the current ecological state towards that long-term expected state. For example, physiological acclimation in plant tissues adjusts the temperature at which photosynthetic efficiency is optimized (Friend, 2010). Environmental filtering of species assemblages reduces the mismatch between the present climate and the community climate niche (Devictor et al., 2008; Gaüzère et al., 2018), potentially maintaining stability and resilience (Carroll et al., 2023). Evolutionary adaptation works by selecting for traits that maximize fitness under present environmental conditions, with the potential rate of evolution being greatest when traits are far from their equilibria (Bürger & Lynch, 1995; Chevin et al., 2010). Higher-order ecological acclimation processes such as turnover in resource pools and shifting disturbance regimes also follow disequilibrium dynamics, due to the interactive effects of physiological acclimation, reordering and turnover in community composition, and evolutionary adaptation.

These ecological acclimation processes occur at vastly different time-scales and are the focus of different disciplines. Physiologists study acclimation in plant tissues occurring on the scale of minutes to days (June et al., 2004; Yamasaki et al., 2002), while paleoecologists study lags between climate change and community assembly over decades and centuries (Davis, 1989; Williams et al., 2002), yet both processes have been characterized by identical differential equations. Specifically, if C is the present climate and E is an ecological state (in units of C), then E tends towards C at a rate proportional to the magnitude of disequilibrium ($C - E$) such that

TABLE 1 Glossary.

Term	Definition	Synonyms and related terms	References
Disequilibrium	The difference between the current ecological state and the state we would expect in the long-term given the current climate	Climate debt, extinction debt, phenotype—environment mismatch	Blonder et al. (2015), Delcourt and Delcourt (1983), Devictor et al. (2012), Felton et al. (2022), Svenning et al. (2015) and Svenning and Sandel (2013)
Ecological acclimation	The collective action of processes that reduce ecological disequilibrium over time	Ecological adaptation, equilibration, thermophilization, tropicalization	Blonder et al. (2017), Carroll et al. (2023), Pinsky et al. (2020), Rosenblad et al. (2023) and Webb (1986)
Acclimation time-scale	The length of time needed for ecological acclimation to reduce disequilibrium by a given proportion	Transient time, lag time, relaxation time	Blonder et al. (2017), Loehle (2018), Ovaskainen and Hanski (2002) and Webb (1986)
Ecoclimate sensitivity	The change of an ecological state or rate in response to a unit of climate change	Climate sensitivity	Bergengren et al. (2011), Lauenroth and Sala (1992), Miller et al. (2018), Williams et al. (2022) and Wolkovich et al. (2014)
Initial sensitivity	The ecoclimate sensitivity observed at the onset of a climatic change	Stationary response	
Transient sensitivity	Any ecoclimate sensitivity observed before an equilibrium is reached (the initial sensitivity is a transient sensitivity)	Nonstationary response, time-varying response	
Equilibrium sensitivity	The ecoclimate sensitivity after ecological acclimation has completed	Asymptotic sensitivity	

$$dE/dt = \frac{1}{\lambda}(C(t) - E(t)), \qquad (1)$$

where λ is the time-scale (in units of time t) of ecological acclimation (Williams et al., 2020). Uses of this equation to represent physiological acclimation (Friend, 2010), community change (Blonder et al., 2017; Webb, 1986) and stabilizing selection (Chevin et al., 2010) feature the same functional form and only differ in the values of the time-scale parameter. This commonality shows that concepts of ecological acclimation and disequilibrium dynamics are not new and are not specific to any single subdiscipline of ecology. A key to this approach is to quantify disequilibrium ($C - E$) by translating the ecosystem state into units of climate; this has been done by quantifying species niches, trait optima and community climate indices (Blonder et al., 2015; Devictor et al., 2008; Eronen et al., 2010). The widely applicable Equation (1) highlights that, in order to anticipate future disequilibrium due to climate change, we need to quantify ecological acclimation time-scales and their predictors, such as generation time, dispersal ability and genetic variation.

The concept of disequilibrium can be useful even if equilibrium is never reached in natural ecosystems. We might never observe equilibrium for at least six distinct reasons: (1) many acclimation processes are slower than the pace of climate change, and climate is ever-changing at multiple scales (Blonder et al., 2018), (2) transient dynamics may lead to absorbing states such as species extinction (Figure S1; Morozov et al., 2024; Ovaskainen & Hanski, 2002), (3) the interactive nature of ecological systems may not produce steady equilibria but instead exhibit complex dynamics such as limit cycles or alternate stable states (Beisner et al., 2003; Scheffer et al., 2012; Turchin & Taylor, 1992), (4) countervailing forces such as acclimation to multiple climate variables or trade-offs between climate-related adaptations and other determinants of fitness may keep systems out of equilibrium with a given climate variable (Hereford, 2009), (5) source-sink dynamics and competition could maintain community climate disequilibrium (Germain et al., 2018; McNichol & Russo, 2023) and (6) disturbance, drift via genetic, environmental or demographic stochasticity (Vellend, 2010), and other perturbations may shift systems away from equilibrium (but see Elvira et al., 2025; Pérez-Navarro et al., 2021). Nevertheless, we can use the concept of climate dis/equilibrium to study, and even quantify, the pace of ecological acclimation (Blonder et al., 2017; Devictor et al., 2008, 2012; Gaüzère et al., 2018).

3 | TRANSIENT AND EQUILIBRIUM SENSITIVITIES

A central question in climate science, first tackled in the 19th century, is how much a doubling of atmospheric CO_2 concentrations would increase mean global temperature. Because the processes driving the feedbacks between temperature and CO_2 concentrations occur at different time-scales, climatologists distinguish between transient and equilibrium climate sensitivities (Armour et al., 2013; Knutti et al., 2017). Transient climate sensitivities are changes in temperature that result soon after a doubling in CO_2 occurs, before the climate system has equilibrated, while equilibrium climate sensitivity is the change in temperature once slow processes have had time to act. Even after CO_2 concentration stabilizes, global temperature may continue to change and sea levels will continue to rise as the atmosphere and oceans mix and other feedbacks run their

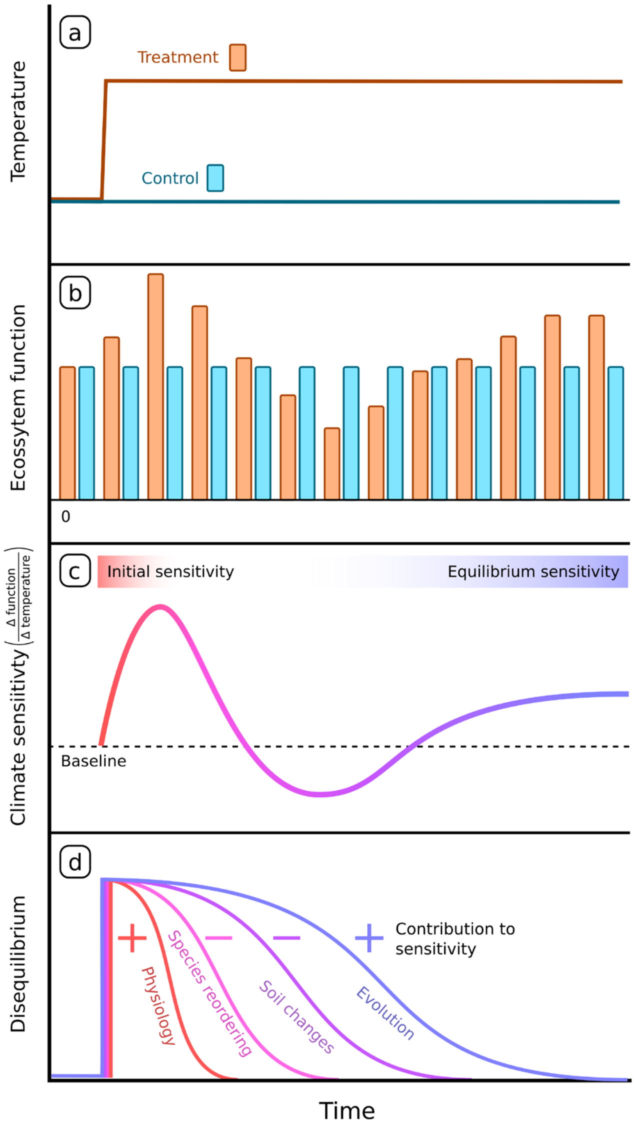

FIGURE 2 Shifting ecoclimate sensitivities are the signature of multiple ecological acclimation processes operating at different time-scales. This figure represents an empiricist's workflow for a hypothetical climate warming experiment in a terrestrial plant community. (a) A warming manipulation is applied to treatment plots alongside control plots where temperature is unchanged. (b) NPP in treatment plots fluctuates over time, but remains constant in the control plots. (c) The ecoclimate sensitivity is calculated as the change in function divided by the change in temperature in each year. Here we show a positive initial sensitivity followed by a transient decrease before arriving at a new steady state above the initial baseline productivity. In the present example, the denominator of the equation does not change because only a single step change in temperature was applied, but the same calculation can be used in the case of continuously changing environmental conditions. (d) Given additional data, we might be able to attribute the shift in ecoclimate sensitivity over time to the action of multiple ecological acclimation processes. The initial transient increase in function could reflect an immediate positive effect of increased temperature on the productivity of thermophilic resident species through physiological changes. Sensitivity may then transiently decrease as populations of heat-intolerant species decline, but new species are slow to arrive due to dispersal limitation. Eventually, adaptive evolution for heat tolerance across resident and newly arrived species and changes in plant functional traits that alter nutrient cycling may lead to a stabilization of ecosystem function, indicating equilibrium sensitivity.

course (Palazzo Corner et al., 2023). Because these processes unfold over long time-scales, equilibrium climate sensitivity may not be observed for millennia.

Similar to climate scientists, ecologists frequently confront protracted responses to environmental change and could benefit from adopting analogous terminology. In the ecological literature, 'ecoclimate sensitivity' refers to the response of an ecosystem property following a change in climate (Bergengren et al., 2011; Williams et al., 2022). Examples may include change in net primary productivity (NPP) per unit of precipitation (g biomass m^{-2} per mm) or change in soil carbon flux per unit of temperature (g C m^{-2} per°C). As with the Earth's climate system, ecosystems respond to perturbations through a suite of processes that range from nearly instantaneous to extremely slow. Following the lead of climate science, we should distinguish between transient and equilibrium ecoclimate sensitivities because they may differ in strength and direction due to contrasting effects of ecological acclimation processes. In the context of global change experiments, the initial sensitivity of an ecosystem to manipulation might be observed in the first year of study, reflecting the action of fast processes such as physiological and demographic shifts. Over multiple years, different transient sensitivities may emerge as slower ecological acclimation processes play out (Figure 2). If the experiment continues for multiple decades, observations may approach the equilibrium sensitivity. Of course, most experiments will never capture the completion of the slowest ecological acclimation processes, and we would need other sources of information, such as biogeographic patterns, to approximate the equilibrium sensitivity.

Distinguishing between initial, transient and equilibrium sensitivities clarifies the conceptual links between the ecological acclimation framework and theory about resistance and resilience. Resistance of an ecosystem function to climate change would occur when the initial sensitivity is weaker than the equilibrium sensitivity. As disequilibrium grows and species approach the limits of their plasticity, systems may lose capacity to resist stress from weather events such as droughts and heat waves (Lloret et al., 2011). Resilience has often been defined as the time needed for a system to return to equilibrium after disturbance (Gunderson, 2000), similar to the concept of ecological acclimation time-scales. Both resilience and the dynamics of ecological acclimation are shaped by past climate conditions and ecological lags (Johnstone et al., 2016). However, resilience is typically thought of as a return to historical equilibrium. The ecological acclimation framework emphasizes that climate change may drive systems towards new equilibria. Positive feedbacks following disturbance can also lead to new equilibria (Scheffer et al., 2012), and disequilibrium due to acclimation lags could tip systems into alternate states (Figure S1).

4 | EXAMPLES OF ECOLOGICAL ACCLIMATION

We present four case studies to demonstrate that the ecological acclimation framework can explain shifting ecoclimate sensitivities observed across a diversity of ecosystems, levels of organization, time-scales and functional responses. Figure 3 summarizes the time-scales of ecological acclimation processes at play in each case study and provides units of the climate and ecological response variables whose quotients determine ecoclimate sensitivities.

4.1 | Plant evolutionary adaptation to drought

Increasing drought frequency and severity put selective pressures on plant populations and may result in transient productivity losses in whole communities. Physiological acclimation and adaptive evolution in response to drought have been well studied in the annual forb *Brassica rapa*, serving as a model of contemporary evolution. The resurrection approach of growing ancestor and descendant populations (Franks et al., 2018) enables comparisons of phenotypes and genotypes before and after drought over multiple decades

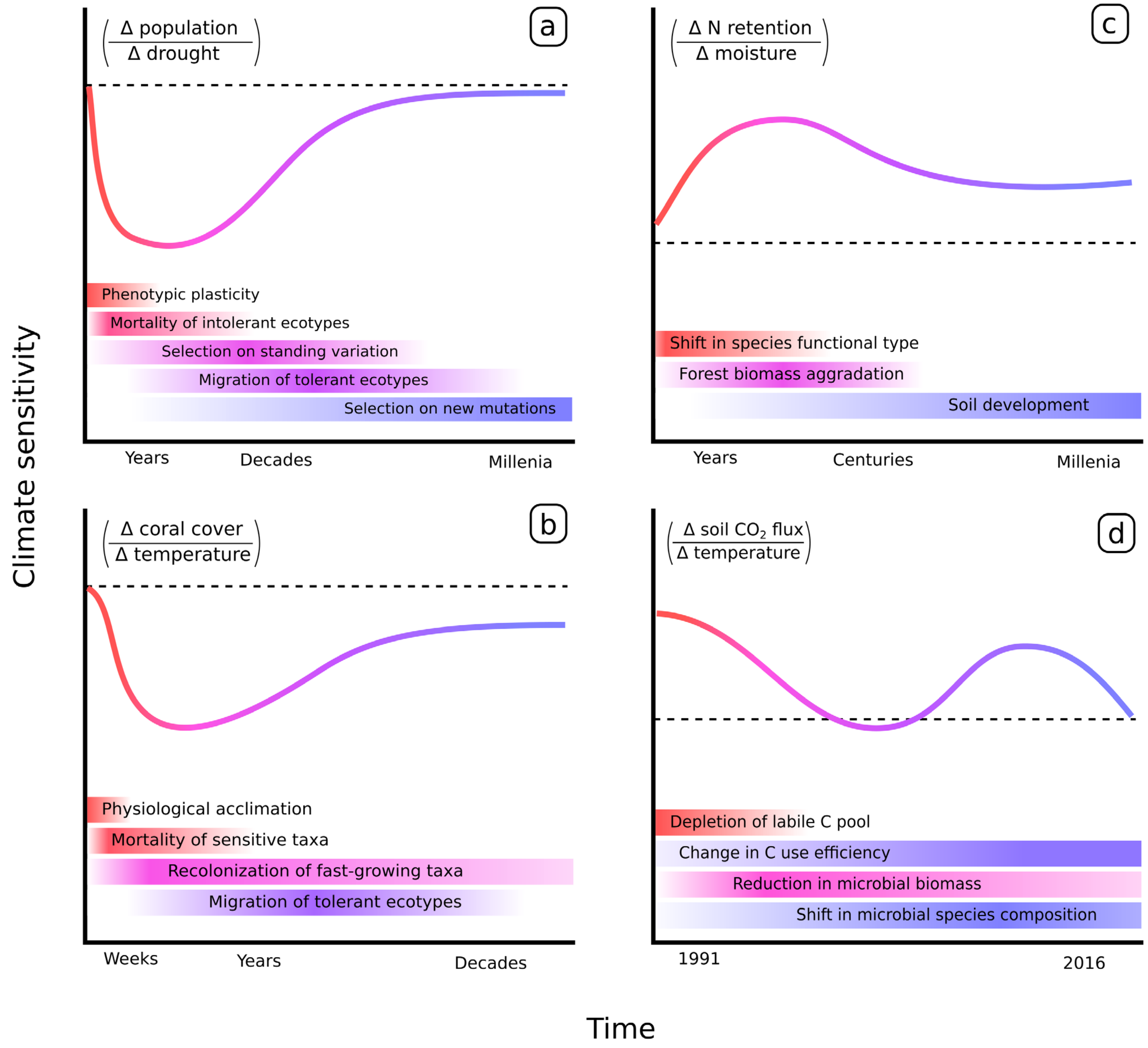

FIGURE 3 Four synthetic examples from various ecosystems demonstrate shifting ecoclimate sensitivities due to acclimation processes operating over different time-scales. (a–d) Correspond to sections 4.1–4.4 in the text. For each case study, sensitivity over time is presented as the change in an ecological response divided by change in a measure of climate change. Horizontal bars represent the timings of the contributions to overall ecoclimate sensitivity of various ecological acclimation processes. Dashed lines mark the baseline sensitivity before the onset of climate change. Colours of the processes and sensitivity curves represent the time-scales of processes at play, with red representing the fastest processes and blue representing the slowest. Refer to the corresponding sections in the text for full descriptions of the various ecological acclimation processes and their effects on overall ecoclimate sensitivity.

(Hamann et al., 2018). Initial sensitivity in population growth rate is shaped by phenotypic plasticity (Johnson et al., 2022) and physiological acclimation of the extant populations over the course of weeks to months (Figure 3a). If droughts exceed the physiological limits of plasticity and physiological acclimation for some individuals in the population, mortality of drought intolerant ecotypes occurs. Transient sensitivity emerges as strong selection on standing genetic variation (Barrett & Schluter, 2008) takes place among remaining individuals, favouring drought-tolerant ecotypes (by way of water use efficiency adaptation and different flowering phenology). This selection results in rapid genotypic frequency shifts over multiple years (Franks et al., 2016) and changes in gene expression through transcriptional responses within generations (Hamann et al., 2021). Transient sensitivity on the time-scale of many years to decades is shaped by migration of drought-tolerant ecotypes through seed dispersal, resulting in gene flow into the population and new phenotypes on which selection can act (Franks & Hoffmann, 2012). Longer-term, equilibrium sensitivity on the time-scale of decades to millennia shifts further due to selection on new mutations for drought tolerance (Bomblies & Peichel, 2022). Given enough adaptation to new precipitation regimes, populations may even recover to historical levels. This scenario of ecological acclimation through multiple processes is contingent on populations persisting at viable levels in the face of increasing drought frequency (Hamann et al., 2018) and other climate changes (Jump & Peñuelas, 2005), such that acclimation is not completely outpaced by climate change.

4.2 | Coral reef acclimation to heat waves

Reef-building corals are suffering a worldwide decline caused primarily by high-temperature anomalies (Hughes et al., 2017). These heat waves disrupt the relationship between corals and endosymbiotic photosynthetic algae. The response of reef corals to heat waves is qualitatively similar to the response of *Brassica rapa* to drought, but depends on processes operating at physiological, genetic and population levels (Figure 3b). At the onset of heat waves, corals cope with thermal stress through physiological acclimation mediated by transcriptomic changes (Bay & Palumbi, 2015; Savary et al., 2021) and through heritable epigenetic effects (Putnam, 2021). These processes shape initial sensitivity on the time-scale of hours to days and allow corals to extend their thermal tolerance during heat exposure. When heat waves persist over longer periods (weeks to months), transient sensitivity emerges as the limits of physiological acclimation are exceeded, and the corals undergo bleaching and mortality due to starvation (McClanahan et al., 2001). The sensitivity of corals to heat waves varies across (Loya et al., 2001) and within species (Dixon et al., 2015), and stress-tolerant corals that survive a heat wave can then help repopulate the reef (Van Woesik et al., 2011). Recolonization is generally slow: many of the most important reef-building corals reproduce once a year, grow slowly and reach sexual maturity within 5–10 years (Rapuano et al., 2023). Even with dispersal of fast-growing coral taxa from neighbouring, intact reefs, full recovery of coral cover may still take over a decade (Gilmour et al., 2013; Gouezo et al., 2019). The transition from transient to equilibrium ecoclimate sensitivity depends on turnover in genotypes and species, from stress-sensitive to more stress-tolerant. As in the drought tolerance case study, this form of acclimation is contingent on the survival of some stress-tolerant individuals.

4.3 | Soil microbiome response to warming

Carbon cycle feedbacks to climate change remain uncertain partly because they unfold over long time-scales. The influence of warming on the respiratory release of CO_2 from soil varies among studies and is complicated by concurrent responses to other global change drivers (Bradford et al., 2016; Carey et al., 2016; Reich et al., 2020). In a landmark study by Melillo et al. (2017), the effects of warming on soil CO_2 fluxes were assessed over 26 years via experimental soil warming (5°C above ambient) in a hardwood forest. This experiment revealed that the sensitivity of soil respiration to warming shifted over time, ranging from positive and neutral to slightly negative, reflecting four distinct phases driven by several interacting biogeochemical acclimation processes (Figure 3c). These dramatic changes in soil CO_2 fluxes through time would have been missed if not for the exceptionally long duration of this field experiment.

Initial sensitivity of soil respiration exhibited a strong, positive response, likely due to the efficient metabolism of the labile carbon pool by soil microorganisms. However, as the labile carbon pool was depleted, soil respiration rates in the warmed plots slowed until they were equivalent to or slightly slower than those in the control plots. This transient depletion was associated with a reduction in microbial carbon-use efficiency (i.e. the proportion of organic carbon taken up that is allocated to microbial growth), a decrease in microbial biomass and reorganization of the microbial community. Subsequently, responses of soil respiration to warming were again positive as microbial community composition shifted towards a higher carbon-use efficiency for recalcitrant substrates like lignin, which became an important carbon source. Finally, microbial biomass continued to decline and soil respiration responses to warming returned to neutral and negative, potentially indicating another transient period of microbial community restructuring and physiological acclimation. It is unclear if the final observations represent equilibrium sensitivity, or if slower ecological acclimation processes would continue to shift the sensitivity. This case study shows how changes in microbial communities may cause complex shifts in ecoclimate sensitivities over a period of two decades; in communities of long-lived organisms, the transition from transient to equilibrium sensitivities might require far more time.

4.4 | Forest development and N cycling following increased moisture

Paleoecological data (e.g. tree rings, lake and mire sediments, and coral deposits) are essential for studying long-term ecological acclimation processes that are too slow to observe in present-day experiments or observational studies (Jackson & Blois, 2015; Nieto-Lugilde et al., 2021). These records have seasonal to decadal temporal resolution and extents of centuries to 10^6 years. Data from Little Windy Hill Pond, a small subalpine lake in southern Wyoming, USA, show how rapid changes in hydroclimate can trigger century-scale transient changes in forest composition, biomass, biogeochemical cycling and fire regime (Kim et al., 2016). A rapid increase in moisture around 11,000 years ago, evidenced by a rise in lake level, triggered a shift from a shrub- to a conifer-dominated community. While the initial transition in plant functional type was rapid enough to track hydroclimate, woody cover and forest biomass continued to increase slowly until 10,000 years before present (Figure 3d). This cascade of ecological acclimation processes resulted in long-term, protracted shifts in nutrient cycling. Levels of δ15N in lake sediments, a proxy for integrated ecosystem N retention (Robinson, 2001), reveal changes in the N cycle following regional climate change. Before the increase in water availability, the system had an 'open' N cycle with low nutrient retention. The initial sensitivity was driven by rapid afforestation and was associated with a transient 'tight' N cycling and strong nutrient retention over roughly 175 years. This resulted from high plant N demand during the period of maximal forest growth, consistent with biogeochemical theory (Vitousek & Reiners, 1975). This period was followed by a transient phase of slow shift back towards lower N retention once mature forest established and N demand for new growth relaxed, although N retention remained higher than prior to afforestation. However, the sensitivity of the N cycle to climate change did not equilibrate after apparent stabilization of forest composition: over the following 1000 years, overall N retention gradually increased further, perhaps as a result of organic matter accrual or reduced fire frequency. Even in the absence of dispersal lags, forest growth produced transient responses in N cycling which continued well after establishment of a new plant community. In summary, the initial, transient sensitivity of N retention reflected decadal-scale changes in vegetation composition, whereas equilibrium sensitivity was a result of centuries of change in forest structure and biogeochemical cycling.

5 | EVIDENCE FOR ECOLOGICAL ACCLIMATION FROM CONTRASTING SPATIAL AND TEMPORAL PATTERNS

The case studies leverage long-term research to demonstrate how ecological acclimation processes play out over multiple time-scales in a variety of ecosystems. A complementary line of evidence for ecological acclimation comes from comparisons of spatial and temporal patterns of ecological sensitivity to climate. While measures of ecoclimate sensitivity from short time-series capture the effect of fast processes such as plasticity, spatial measures represent slower processes such as local adaptation (Ramirez-Parada et al., 2024), and the two are often drastically different. For example, spatial networks of tree-ring time series show that the growth of many tree species decreases in years of high temperatures, whereas the average growth rate at different locations across a region increases with mean temperature (Buechling et al., 2017; Canham et al., 2018; Klesse et al., 2020; McCullough et al., 2017). That is, trees grow more slowly in warmer-than-average years even though they grow faster at warmer-than-average locations (Perret et al., 2024). Similarly, mean net primary productivity in semiarid ecosystems increases across spatial gradients of increasing mean annual precipitation, but at any one site, the relationship between interannual variation in precipitation and productivity is much weaker (Huxman et al., 2004; Lauenroth & Sala, 1992). Dramatic contrasts between spatial and temporal responses to climate drivers have also been observed in populations of birds (Bradter et al., 2022; Gaüzère & Devictor, 2021; La Sorte et al., 2009), amphibians (Miller et al., 2018), mammals (Billman et al., 2023), shrubs (Kleinhesselink & Adler, 2018) and alpine plants (DeMarche et al., 2021; Oldfather et al., 2021).

What do these contrasting patterns have to do with ecological acclimation? Spatial, biogeographic patterns reflect acclimation processes that have played out over long time-scales. For example, xeric and mesic grassland sites differ dramatically in species composition, functional diversity, soil structure and natural disturbance regimes. All of these differences, which develop over centuries to millennia in response to sustained differences in climate, affect primary productivity. Therefore, the slope of the relationship between mean productivity and mean annual precipitation observed across a spatial gradient represents the long-term response of all ecological acclimation processes to climate, approximating an equilibrium sensitivity (Figure 4). In contrast, longitudinal studies of interannual variation in precipitation and grassland productivity hold species composition, soils and disturbance regimes relatively constant, and interannual variation in productivity will reflect processes fast enough to drive changes from 1 year to another, such as physiological and phenological plasticity. The slope of the relationship between annual precipitation and annual productivity at one site in the short term (several years to a few decades) represents a transient sensitivity (Figure S1). Given a long-term shift in mean annual precipitation, we would expect that transient sensitivity to change, perhaps over multiple decades.

Comparisons of spatial and temporal patterns reveal the shifting impact of acclimation processes across time-scales (Figure 4). The greater the difference between the apparent equilibrium sensitivity, represented by the spatial pattern, and the initial transient sensitivity, represented by the temporal pattern, the greater the impact of slow acclimation processes. On the other hand, spatial and temporal patterns that are qualitatively and quantitatively similar suggest that slow acclimation processes have little effect on the ecological response of interest or that their overall effect is similar to that of faster processes. While these comparisons can measure the magnitude of differences between transient and equilibrium sensitivities, they do not provide information about the temporal scale of the acclimation processes that generate those differences. Therefore, comparisons of spatial and temporal patterns are a useful first step to identify situations in which surprising changes in ecological

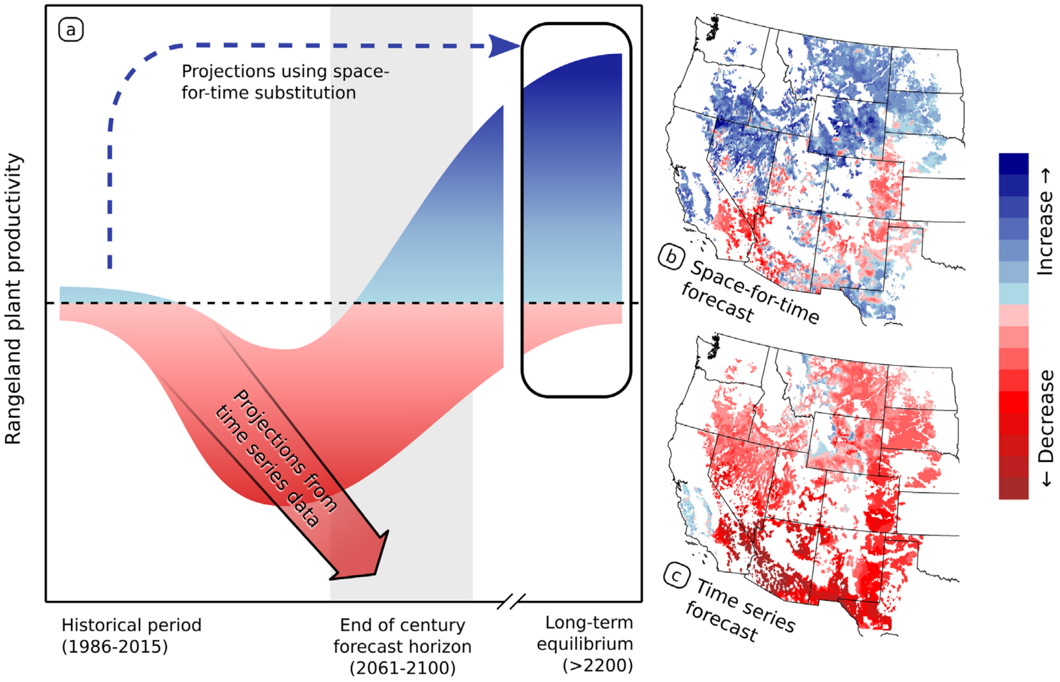

FIGURE 4 Ecological acclimation is expected to shift ecoclimate sensitivities over time (coloured curve). Common modelling approaches make implicit assumptions about ecological acclimation time-scales, resulting in conflicting predictions about ecological responses to climate change (a). Projecting far into the future from models fit to short-term time-series data assumes that initial sensitivities are permanent and that slow ecological acclimation processes will not influence long-term dynamics (red arrow). When used to forecast rangeland forage production in the western United States, this method predicted widespread declines by the end of this century (c, lower map). On the other hand, models that rely on space-for-time substitution fail to capture transient dynamics because they assume that even slow ecological acclimation processes will happen quickly, keeping pace with climate change (blue arrow). This method predicted increases in plant productivity in many regions, reflecting long-term equilibrium expectations (b, upper map). The magnitude of discrepancies between time-series and space-for-time forecasts represents the uncertainty associated with the actual pace of ecological acclimation. Maps are adapted from Felton et al. (2022).

response may play out over time and stimulate further research on acclimation rates, potentially using the approaches illustrated in the case studies. If the time-scales of ecological acclimation processes are known, then the difference between temporal and spatial patterns could be informative about the impact of disequilibrium on the ecological response variable in question.

6 | MODELS AND IMPLICIT ASSUMPTIONS ABOUT ACCLIMATION TIME-SCALES

Correlative models used to project long-term ecological impacts of climate change typically make implicit and often problematic assumptions about ecological acclimation processes (Figure 4). For example, models based on empirical relationships estimated from short-term experiments or relatively short observational time series will feature the influence of fast but not slow processes. Long-term projections based on these models assume that transient sensitivities are permanent (i.e. ecosystems are stationary). On the other hand, predictions from models based on spatial patterns, like the use of species distribution models to predict future ranges without taking lags into account (Essl et al., 2023), effectively assume that responses will instantly reflect equilibrium sensitivities (which is why many practitioners emphasize that distribution models predict potential habitat suitability, not distribution). If the transient and equilibrium sensitivities are very different, then projections based on one or the other will also differ dramatically (e.g., Perret et al., 2024), leading to high uncertainty. In fact, a recent study projecting future rangeland forage production found that uncertainty related to contrasting assumptions about ecological acclimation time-scales was similar to, or even greater than, uncertainty coming from variation among greenhouse gas emission scenarios or general circulation models (Felton et al., 2022; Figure 4).

In principle, process-based ecosystem models should be able to capture both transient and equilibrium sensitivities. For example, dynamic global vegetation models could simulate the changes in plant functional group composition that lead to shifting sensitivities (Snell et al., 2014). In practice, however, these models often rely on the same assumptions embedded in correlative models and may not reflect shifting sensitivities (Fisher & Koven, 2020). When parameters in process-based models are derived from relatively short-term, longitudinal data, such as eddy flux tower data, they will capture transient sensitivities but will exclude slow acclimation processes (e.g. Rollinson et al., 2017). When these models are trained with data describing biogeographic patterns (Fisher et al., 2015), they will capture equilibrium sensitivities but not the transient lags. Even if both kinds of data are used to inform parameters, current process-based terrestrial ecosystem models may lack the fine-scale spatial, temporal and taxonomic resolution needed to represent both slow and fast acclimation processes (e.g. demography, evolution). Finally, process-based ecosystem models often contain many parameters that are difficult to estimate. Focusing on ecological acclimation time-scales (λ, Equation 1) offers a parsimonious, phenomenological approach for anticipating the shift from transient to equilibrium sensitivities.

7 | MODELS NEED TO ACCOUNT FOR DISEQUILIBRIUM DYNAMICS

No single model can include all the relevant processes needed to accurately forecast from very short to very long horizons. The challenge is to make sure that models include the processes relevant to a particular forecast horizon and to make those in/exclusions explicit (Adler et al., 2020). In other words, the time-scales of acclimation processes captured by a model should match the time-scales of predictions made by that model (Figure 1). Models of initial transient sensitivity to climate change (e.g. those based on responses to weather fluctuations) will be most useful when forecasting several months or years into the future. This is the realm of iterative ecological forecasting, where predictions can be evaluated on time-scales that are short enough to be fed back into the model development workflow (Dietze et al., 2018). Models that represent equilibrium sensitivities to climate change (e.g. those based on geographic climate gradients) will be more appropriate for forecasting the state of ecosystems many decades or centuries in the future.

Predictions for forecast horizons encompassing the transition from initial to equilibrium sensitivities will be uniquely challenging. At these medium forecast horizons (multiple decades), slow acclimation processes could have a strong influence on the ecological response, but have not yet approached equilibrium (Figure 4). Moreover, the interaction of multiple ecological acclimation processes may result in unexpected and consequential transient dynamics (Francis et al., 2021) that are substantially different from both initial and equilibrium patterns. This problem is not unique to ecology: intermediate forecast horizons are also a challenge in atmospheric science. Meteorological models forecast weather reliably out to 1–2 weeks, and general circulation models make consistent predictions about the effects of changes in greenhouse gas concentrations on long-term climate, but neither approach handles seasonal to decadal scales well (Bauer et al., 2015). Making predictions that account for a suite of processes across a range of acclimation time-scales may require phenomenological modelling of disequilibrium dynamics (Blonder et al., 2017; Equation 1), incorporating various acclimation processes into mechanistic ecosystem models (Harrison et al., 2021) or adopting a scheme in which the weighted contribution of different processes shifts over time (Adler et al., 2020).

Accounting for acclimation processes and shifting sensitivities will also be important in models of social–ecological systems. For example, marine fish populations and fishing activity along the US Atlantic coast have both shifted northward in recent decades, with ecological, abiotic and institutional constraints determining the rate of change (Dubik et al., 2019). Social–ecological interactions operate over a wide range of time-scales, and—similarly to ecological processes—the time-scales of long-term changes in human systems are poorly understood, inherently uncertain and rarely included in predictions of long-term environmental change (Ward et al., 2019). But human decision-making often operates on faster time-scales than the corresponding ecological processes (Wilson et al., 2016), a mismatch that can lead to adverse social and ecological outcomes, as in the 1930s Dust Bowl in the U.S. Great Plains (Peters et al., 2007). Like their counterparts modelling purely biological systems, modellers of social–ecological systems should take care to match the time-scales of their predictions with the time-scales of the acclimation or adaptation processes featured in their models.

Regardless of the kind of model used or the goal of prediction, researchers must clearly communicate the processes that are and are not captured in their projections in order to clarify the time-scales at which the projections are relevant. For example, projections of habitat suitability using species distribution modelling can be explicit about the consequences of limited range shifts, local evolutionary adaptation and their interaction (Schuetz et al., 2015). More broadly, assumptions about ecological acclimation time-scales should be made explicit to clarify the applicability and transferability of space-for-time substitutions in global change studies (Lovell et al., 2023). The concept of ecological acclimation provides a framework that facilitates clear communication about the many processes that influence how ecological systems respond to changing climate. When the time-scales of the potentially relevant acclimation processes are uncertain, further research (e.g. Mottl et al., 2021) will be needed to determine if sensitivities are likely to change within the temporal scope of the desired prediction.

8 | MANAGEMENT IMPLICATIONS

Natural resource managers are already working with concepts central to the ecological acclimation framework to address challenges imposed by climate change. Adaptive capacity is recognized as a key factor in reducing ecosystem vulnerability to climate change (Glick et al., 2011; Thurman et al., 2020, 2022), underscoring the importance of ecological acclimation processes. Furthermore, anticipatory management seeks to inform decisions with predictions across a wide range of time-scales (Bradford et al., 2018). As ecological nonstationarity changes the efficacy of traditional management practices, managers are grappling with whether—and under what conditions—to resist, accept or direct the trajectory of ecological change (Lynch, Rahel, et al., 2022; Schuurman et al., 2022). The ecological acclimation framework can aid these efforts to make management responsive to forecasted ecological changes.

When climate change outpaces the ability of ecological acclimation to maintain ecosystem services (Carroll et al., 2023), understanding and potentially accelerating acclimation processes will become increasingly important. In addition to the negative effects of disequilibrium on ecosystem services, the transient dynamics they generate may reduce capacity for future ecological acclimation if species become extirpated, genetic diversity is lost or the ecosystem enters a degraded alternate state (Beisner et al., 2003; Morozov et al., 2024). For example, coral reef recovery following heat waves (Figure 3b) is contingent on the persistence of some heat-tolerant taxa to reestablish the community. Management interventions such as assisted migration (Hällfors et al., 2017) and assisted evolution (Van Oppen et al., 2015) that act by accelerating ecological acclimation could minimize losses of ecosystem services by easing transitions (Millar & Stephenson, 2015). Research to quantify acclimation time-scales could help focus limited resources for management interventions on the slowest-acclimating ecosystems (Hällfors et al., 2017). Identifying which ecological acclimation processes are most influential across populations may also inform management for species whose responses to climate differ throughout their geographic ranges (Gavin & Hu, 2006). This could help mitigate the transient risk of extirpations due to acclimation lags at the edges of species distributions (Evans et al., 2024; Figure S1).

Managers often rely on scenario-based approaches to guide decision-making (Rosa et al., 2017), but developing scenarios that represent the tremendous uncertainty about long-term ecological impacts of climate change is a challenge. An explicit consideration of ecological acclimation could help clarify the range of plausible future scenarios (Schuetz et al., 2015) and inform decisions about resisting, accepting or directing change at various time horizons (Lynch, Thompson, et al., 2022). Accounting for acclimation processes may not only reveal uncertainties hidden by models that make implicit assumptions about climate disequilibrium (Felton et al., 2022) but could also help managers identify a wider range of possible management strategies.

Adaptive management, an iterative approach to decision-making in the face of uncertainty, seems like a natural way to incorporate acclimation processes in management (Williams & Brown, 2018). However, ecological stationarity often remains an underlying assumption in adaptive management programmes (Lynch, Thompson, et al., 2022). Crucially, because transient sensitivities are often different from equilibrium sensitivities, management practices that are adjusted based on initial, short-term monitoring may be counterproductive to long-term goals (Hastings, 2016). For example, initial poor performance of plant restoration may be influenced by lags in the formation of mycorrhizal associations (Neuenkamp et al., 2019; Wall et al., 2020). In this case, the time-scale of fungal community assembly can be accelerated—and the undesirable transient period shortened—through soil inoculation (Koziol & Bever, 2017). Ideally, adaptive management should account for mismatches between the timesteps of iterative monitoring and the time-scales of ecological acclimation processes (Wilson et al., 2016).

9 | ROADMAP FOR FUTURE RESEARCH

A research agenda focused on ecological acclimation time-scales will help reduce uncertainty in medium to long-term forecasts of climate change effects on ecosystems. We hope that the ecological acclimation framework will inspire new lines of inquiry and promote synthesis of existing knowledge across disciplines with unifying concepts and vocabulary. Here, we outline the most immediate priorities.

First, we need a new theory. Because ecological acclimation encompasses so many processes, from evolutionary adaptation to biogeochemical feedbacks, a fully mechanistic treatment is intractable. Instead, we need simple models (e.g. Equation 1) to describe the common features of acclimation dynamics (i.e. reduction of disequilibrium over time) that operate across spatial and temporal scales and levels of biological organization. Such a theory will facilitate communication among researchers working in different subdisciplines and will provide tools to estimate the time-scale and impact of acclimation processes in empirical data. There is a base of quantitative tools for characterizing disequilibrium in community composition (Blonder et al., 2015; Devictor et al., 2008) and phenomenological theory for how community dynamics reduce disequilibrium in turn (Beaugrand, 2015; Blonder et al., 2017; Bonachela et al., 2021; Gaüzère et al., 2018; Webb, 1986). We need to extend this to additional acclimation processes beyond shifts in community composition.

Second, we need to apply this new theory to describe cross-system variation in acclimation rates and their impacts on ecosystem functioning. This kind of quantitative synthesis is already within reach for research on climate disequilibrium in species composition thanks to the rapid accumulation of case studies (e.g. Pérez-Navarro et al., 2021; Richard et al., 2021; Rosenblad et al., 2023; Sharma et al., 2022). The next challenge is to identify the factors that determine acclimation time-scales and their ecosystem impacts. Generating hypotheses is easy. For example, we expect that dispersal rates and distance to source populations, generation time, niche breadth, the strength of selection, disturbance frequency, the magnitude of temporal climate variation and the rate of climate change could all influence the rate of community turnover. Or we might expect that the sensitivity of ecosystem function to climate is shifting most rapidly in systems with the highest rates of compositional change. While testing such hypotheses is much harder, the increasing availability of archived field data and remotely sensed data offers opportunities.

Finally, we need to consider interactions among multiple acclimation processes. In the present case studies, we mostly discussed ecological acclimation processes as if they were independent, but in many cases, they will act synergistically or antagonistically. Evolutionary adaptation is expected to slow species turnover when it helps the dominant species, but should accelerate species turnover if it has a greater relative effect on the fitness of subordinate species or potential colonists (Valladares et al., 2014). Changes in disturbance regimes, like increases in fire severity, could accelerate species turnover (Pérez-Navarro et al., 2021; Tanner et al., 2022;

Williams et al., 2020), or changes in biogeochemical cycling (Pellegrini et al., 2018) could feed back to influence disturbance regimes themselves. Understanding these interactions will improve our ability to predict rates of ecological acclimation.

10 | CONCLUSION

Accurate forecasts and anticipatory management of ecosystems will require interdisciplinary collaboration among climate scientists, natural resource managers, evolutionary biologists and ecologists who focus on disparate processes. The ecological acclimation framework should facilitate this interdisciplinary synthesis by providing a common vocabulary and set of fundamental concepts. Disequilibrium between ecosystems and the climate has the potential to produce unexpected transient dynamics that are difficult to anticipate from short-term observations. The rates at which disequilibria are created and then reduced by acclimation processes will play a major role in determining the ecological consequences of climate change. A focus on the time-scales and ecosystem impacts of acclimation processes will help researchers and managers reduce uncertainty about the future and make robust decisions to minimize the negative effects of climate change.

AUTHOR CONTRIBUTIONS

All authors conceptualized this work and contributed to editing the manuscript. Michael Stemkovski and Peter B. Adler wrote primary drafts. Loretta C. Johnson, Brooke B. Osborne, Oliver Selmoni and Kyra Clark-Wolf drafted the case studies. Michael Stemkovski, John B. Bradford, Abigail J. Lynch, Christine R. Rollinson and Peter B. Adler organized the working group.

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ACKNOWLEDGEMENTS

This work was funded by NSF BoCP grant number 204754. We thank Nicolas Matallana, Annie Schiffer, Megan Vahsen and Shelley Crausbay for providing helpful reviews of an earlier draft of this paper. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. ORNL is managed by UT-Battelle, LLC, for the DOE under contract DE-AC05-100800OR22725. This research was supported by the Utah Agricultural Experiment Station, Utah State University, and approved as journal paper number 9900.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

We have no data or code to share.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Forecasts based on spatial and temporal measures of ecoclimate sensitivity make different implicit assumptions about ecological acclimation timescales.

How to cite this article: Stemkovski, M., Bernhardt, J. R., Blonder, B. W., Bradford, J. B., Clark-Wolf, K., Dee, L. E., Evans, M. E. K., Iglesias, V., Johnson, L. C., Lynch, A. J., Malone, S. L., Osborne, B. B., Pastore, M. A., Paterson, M., Pinsky, M. L., Rollinson, C. R., Selmoni, O., Venkiteswaran, J. J., Walker, A. P., … Adler, P. B. (2025). Ecological acclimation: A framework to integrate fast and slow responses to climate change. *Functional Ecology*, *00*, 1–17. https://doi.org/10.1111/1365-2435.70079