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PERSPECTIVE

Linking Community-Climate Disequilibrium to Ecosystem Function

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ABSTRACT

Turnover in species composition often lags behind the pace of climate change, resulting in mismatches between climate and communities. However, the impact of these community-climate disequilibria on ecosystem functions is rarely considered, and current methods for measuring disequilibria assume that species ranges were, until recently, in equilibrium with climate. Here, we develop a simple theoretical model to address both of these problems by linking community-climate disequilibrium with ecosystem functioning. We show how disequilibrium can impair functioning in the near-term even when climate change is expected to enhance functioning in the long-term. Responses are most likely to change over time in communities where turnover is slow, the impact of disequilibrium counteracts the direct effects of climate on ecosystem function, and pre-existing disequilibrium is large. These findings emphasise the importance of precise and unbiased estimates of community-climate disequilibria for improving ecological forecasts. By fitting our model to time series of both climate and ecosystem function from a metacommunity simulation, we show the potential for community-climate disequilibrium to be inferred without direct knowledge about species' distributions or climatic tolerances. We end by outlining a research agenda to apply dynamic disequilibrium concepts and test novel hypotheses across diverse ecosystems.

1 | Introduction

Climate change is already causing strong directional shifts in many ecological communities. Changes in species abundances, along with immigration and local extinction events, have produced more warm-tolerant species assemblages (Devictor et al. 2008; Pérez-Navarro et al. 2024; Rosenblad et al. 2023; Zarzyczny et al. 2024). However, rates of compositional change vary due both to the pace of climate change and the rate at which communities can respond. For example, species' ranges have tended to shift most rapidly where climate is changing fastest (Lenoir and Svenning 2015; Martins et al. 2024; Sunday et al. 2015; Williams and Blois 2018), and for species with shorter generation times (Compagnoni et al. 2021). Where rates of community change are too slow to track climate change, mismatches may develop between the present climate and the species composition of the community (Alexander et al. 2018). We call this mismatch *community-climate disequilibrium*, and it can be calculated as the difference between the community-level average of species' climate niche optima and the climate experienced by the community (Stuart-Smith et al. 2015; Svenning and Sandel 2013; Williams et al. 2020). Community-climate disequilibria resulting from recent climate change are often large in forests (Rosenblad et al. 2023; Zhu et al. 2012), but smaller in communities of annual plants (Martin et al. 2019; Zhu et al. 2024) and mobile marine organisms (Lenoir et al. 2020; Pinsky et al. 2013).

Evidence that community-climate disequilibria are common across diverse ecosystems (Aguirre-Gutiérrez et al. 2025; Schweiger and Svenning 2024) raises the question: What are the consequences of community-climate disequilibrium for ecosystem functioning? Populations' fitness suffers when they are far from their climate optima (Thuiller et al. 2005; Valladares et al. 2014), but does this pattern extend to the community level? To date, community-climate disequilibrium has primarily been used to summarise changes in community structure over time (Devictor et al. 2012; Rosenblad et al. 2023; Zhu et al. 2012, 2024), but the potential of the concept for predicting ecosystem functions such as primary productivity, carbon sequestration and decomposition rates has not been fully realised (but see Felton et al. 2022; Glassman et al. 2018; Wang and Allison 2022). Identifying the communities that are most likely to experience loss of function due to disequilibrium can help inform choices about whether—and how—to resist, accept, or direct ecological responses to climate change to maintain nature's contributions to people (Bradford et al. 2018; Lynch et al. 2022).

Linking community-climate disequilibria to ecosystem functioning could also help explain surprising observations from global change experiments. Multiple studies have found that initial and long-term ecosystem responses to warming and CO_2 treatments differ in magnitude and even direction (Harte et al. 2015; Melillo et al. 2017; Reich et al. 2018; Reich and Hobbie 2013). For example, in situ warming of an alpine meadow caused rapid initial losses of soil organic carbon, but the effect diminished after a decade and had nearly disappeared after two decades of elevated temperatures as shrubs replaced forbs and produced more recalcitrant litter (Harte et al. 2015). A model based only on the initial, or short-term, response to warming would fail to predict the observed long-term changes in soil carbon. In this experiment, the change in soil carbon dynamics reflected decadal-scale shifts in species composition, as drought-intolerant forbs declined and shrubs increased. Slow, multidecadal changes in species composition in response to climate change could offer a general explanation for the non-monotonic dynamics in ecosystem functions observed in experiments. More broadly, accounting for lagging changes in communities may be the key to accurately forecasting climate change impacts on ecosystem functioning.

Here, we propose a new, theoretical modelling framework to investigate and ultimately predict the consequences of community-climate disequilibrium for ecosystem functioning. Our goal is to integrate previously disparate lines of research: while community responses to climate change and the equilibrium relationships between climate and ecosystem functioning have received considerable attention, the effect of community-climate disequilibrium on ecosystem functioning has not. The framework we offer posits that community-climate disequilibrium can alter the sensitivity of ecosystem functions to climate (Figure 1). Simple, phenomenological models built on this premise can advance research in two ways: (1) They can help us predict complex, transient dynamics in ecosystem responses to climate change; (2) they make it possible to use information about ecosystem functioning to improve inference about rates of community change.

We demonstrate these two applications of the framework as follows. Section 2 provides a mathematical definition of community-climate disequilibrium and background on an existing model of

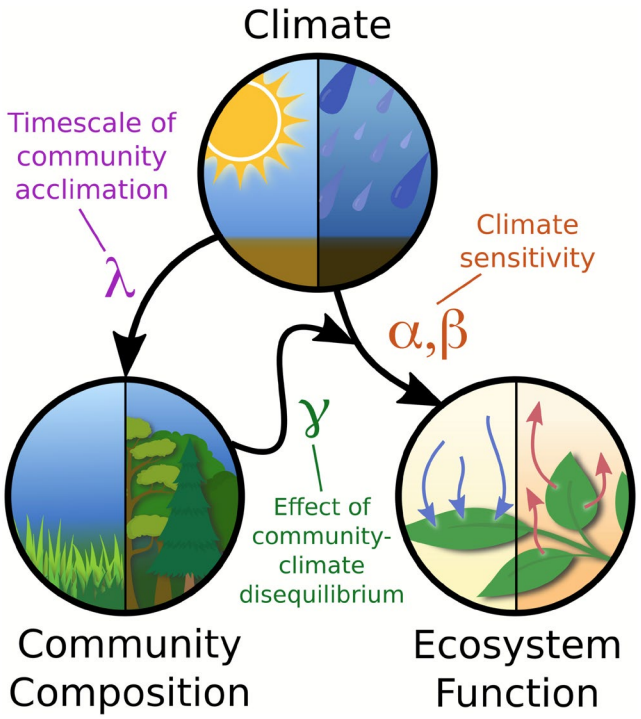

FIGURE 1 | Conceptual representation of the relationships between climate, community composition, and ecosystem function. Communities respond directly to climate change through community acclimation (Equation 1, defined in Section 2), and ecosystem function is sensitive to climatic variation and change (Equation 2). Disequilibrium between communities and the climate modifies the climate sensitivity of ecosystem function (Equation 3).

community acclimation dynamics. Section 3 develops a novel, phenomenological modelling approach that relates community-climate disequilibrium with ecosystem functioning with a minimal number of parameters. We analyse multiple variants of this model to answer the question, when should we expect complex, non-monotonic ecosystem responses to monotonic climate change? Section 4 shows how our approach could enable inference about community change from time series data on climate and ecosystem functioning without making the common assumption that species ranges are in equilibrium with climate. In Section 5, we generate data from a relatively mechanistic metacommunity simulation to offer a proof-of-concept that our community-climate disequilibrium model can account for emergent, transient dynamics of ecosystem function while also providing inference about community composition. Section 6 proposes a research agenda to apply the wealth of data on community-climate disequilibria to improve predictions about the effects of climate change on ecosystem functions. Our intention is not to provide definitive statistical tools, but to spur new research by formalising hypotheses about the links between ecosystem structure and function in the context of climate change.

2 | Background: Community-Climate Disequilibrium and Acclimation Dynamics

Ecological communities broadly reflect the climate in which they are found (Lomolino et al. 2010), but communities do not respond instantaneously to rapid changes in climate (Davis 1986). To study the consequences of mismatches between the pace of climate change and community responses, we need to understand how community-climate disequilibrium changes through time. Although climate forcing is not the only factor shaping communities, changes in community composition will reduce disequilibrium over time when individuals of species that are poorly adapted to the present climate are outcompeted by those that are better adapted (Ordonez and Svenning 2020). In other words, communities 'acclimate' to climate change through increases in the relative abundance of species whose niches better match the new climate (Carroll et al. 2023; Vellend 2010). We define *community acclimation* as the joint action of climate-driven species abundance reordering, immigration and extirpation which collectively shift community climate niches closer to the present climate (Stemkovski et al. 2025).

One approach to quantify the climate to which a community is best suited is to average across species' realised climate niche optima to calculate the community climate niche. Widely used examples include the Community Temperature and Precipitation Indices (CTI & CPI) (Blonder et al. 2015; Devictor et al. 2008). Related approaches are used to infer past climate from species assemblages while accounting for species interactions (Bertrand et al. 2011; Liu et al. 2020). If E is the community climate niche and C is the climate experienced by the community at a given time, then community-climate disequilibrium is $C-E$. Critically, this comparison is possible because both variables are in units of climate. The rate of change in the community climate niche E over time t can be expressed with the differential equation,

$$\frac{dE}{dt} = \frac{1}{\lambda}(C(t) - E(t)), \quad E(0) = E_0, \tag{1}$$

where λ is the timescale of community acclimation in units of time t (the time needed to reduce community-climate disequilibrium by a factor of e), and E_0 is the initial community climate niche value (Blonder et al. 2017; Webb 1986). This equation posits that the rate of community acclimation is proportional to community-climate disequilibrium: communities close to equilibrium with climate (small $|C-E|$) will change slower than those that are severely mismatched with climate (large $|C-E|$). Smaller values of λ represent fast-acclimating communities most likely to track climate change, and greater values represent communities that may lag behind (Figure 2a). The magnitude of community-climate disequilibrium will be greatest when climate change is fast and community acclimation is slow (Williams et al. 2020) (Figure 2b).

Most communities are not in equilibrium with climate due to numerous factors including historical climate legacies, recent climate change, disturbance and biotic interactions that counteract climate-driven community assembly (Alexander et al. 2018; Blonder et al. 2018; Devictor et al. 2012; Perez-Navarro et al. 2022; Rosenblad et al. 2023). Thus, Equation (1) allows for initial community-climate disequilibrium ($E_0 \neq C(0)$). This formulation enables us to parse the degree to which observed shifts in community composition are due to ongoing climate change versus historical climate legacies (Blonder et al. 2018; Svenning et al. 2015).

Equation (1) was first applied in a (paleo-)ecological context by Webb (1986) to model vegetation dynamics in response to climate change during the Quaternary Period, and it is inspired by Newton's law of cooling, which describes how the reading of a thermometer lags behind ambient temperature (Middleton et al. 1938). Calculating a community climate niche is analogous to 'taking the temperature' of a community, and tracking community-climate disequilibrium dynamics is like waiting for a thermometer to show an accurate reading. Equation (1) is only one possible functional form for community acclimation; the dynamics of variants are discussed by Blonder et al. (2017).

Mismatch between species composition and climate is only one of many disequilibria in ecological systems (Stemkovski et al. 2025). Similar disequilibrium concepts and dynamical models have been used to describe plant physiological plasticity (Friend 2010), adaptive trait evolution (Chevin et al. 2010), and animal thermoregulation (Rezende and Bacigalupe 2015). Although numerous biotic factors and interacting climate dimensions drive the dynamics of ecological acclimation, in this paper we focus on the consequences of climate-driven turnover in community composition.

3 | Modelling the Effects of Community-Climate Disequilibrium on Ecosystem Function

To link community-climate disequilibrium to ecosystem functioning, we start with a linear equation that does not consider the community state,

$$F(t) = f(C(t)) = \alpha + \beta C(t), \tag{2}$$

where the sensitivity of an ecosystem function F to climate C at time t is represented by the slope parameter β, with a baseline level of functioning α. Equation (2) can be viewed as an equilibrium expectation which assumes that climate change either never

produces community-climate disequilibrium or that ecosystem function is unaffected by disequilibrium. Such linear equations are commonly used to characterise the relationship between ecosystem function and climate (Sala et al. 1988), but nonlinear forms may be more appropriate when considering wider climate ranges. For example, the sensitivity of primary productivity to precipitation weakens as water availability increases, a pattern captured by the saturating functional form $\kappa(1-e^{-\beta C})$ (Huxman et al. 2004), which our framework can accommodate (Appendix S1: Sections S1.1 and S3).

We incorporate disequilibrium by assuming that communities far from equilibrium with climate are composed of species with reduced fitness and functioning due to suboptimal conditions. For example, whole-community turf transplant experiments show that communities often exhibit diminished functioning in climates to which they are poorly suited (Block et al. 2022; Ma et al. 2022). Thus, we expect functioning ($F(t)$) to decrease as disequilibrium ($C(t)-E(t)$) increases in many communities. We represent the effect of community-climate disequilibrium on ecosystem function by modifying the slope of climate sensitivity in Equation (2):

$$F(t) = g(C(t), E(t)) = \alpha + \left(\beta - \gamma(C(t)-E(t))^2\right)C(t). \quad (3)$$

Here, γ determines the effect of disequilibrium ($C(t)-E(t)$) on climate sensitivity. When there is no disequilibrium ($C(t)-E(t)=0$), Equation (3) reduces to Equation (2). Disequilibrium is transformed using a quadratic loss function because we expect both extreme positive and negative disequilibria to impact ecosystem function (Figure 2d). Although we expect high disequilibrium to reduce functioning in many communities, this is not a necessary feature of the model; disequilibrium that boosts ecosystem functioning is represented by a γ value of opposite sign. The main point is that disequilibrium can modify the equilibrium climate sensitivity of ecosystem function (Equation 2). It is critical to consider both the direct equilibrium sensitivity (β) and the mediating disequilibrium effect (γ) together, as strong equilibrium sensitivities can outweigh disequilibrium effects, and vice versa (note how F is maximised when $C > E$ due to positive β in Figure 2d). The effect of disequilibrium can be incorporated in different ways to match ecological assumptions and use cases, yielding alternative forms of Equation (3). We discuss the assumptions and potential use cases of several functional forms, including ones featuring nonlinear equilibrium climate sensitivity, in the supplement (Section S1.1: Appendix S1 and Table S1). We also encourage readers to explore the dynamics of these equations in an accompanying R-Shiny app (https://www.stemkovski.com/visualizations/ecological-acclimation-app).

The system of Equations (1) and (3) predicts that climate change could cause transient losses in function even when the long-term equilibrium expectation is enhanced function (Figure 2c). Such dynamics occur when community acclimation lags behind climate change and disequilibrium grows to the point that its effect outweighs the direct sensitivity of ecosystem function to climate. Moreover, it predicts that a linear, monotonic change in climate could produce a nonlinear ecosystem function response that changes from negative to positive (or vice-versa) over time. In fact, quadratic (Harte et al. 2015) and even cubic (Melillo et al. 2017) soil carbon responses have been observed in long-term warming experiments. But how likely are these sign-switches? When should we expect complex, non-monotonic ecosystem responses to climate change?

To answer these questions, we analysed the temporal dynamics of ecosystem function for a variety of possible relationships between ecosystem function and climate, community climate niches and community-climate disequilibrium. Here, we use 'temperature' as a stand-in for any hypothetical climate variable that influences community composition and ecosystem function. For all forms of Equation (3) (Table S1), we found large regions of parameter space where ecosystem function can have non-monotonic responses to either a discontinuous or a continuous linear increase in temperature (Section S2: Appendix S1). When temperature changes abruptly, as in a warming experiment, ecosystem function responses are non-monotonic whenever community-climate disequilibrium immediately after the temperature increase is sufficiently large: an immediate, discontinuous decrease in ecosystem function is followed by a continuous increase (Section S2.1: Appendix S1). When temperature increases gradually, non-monotonic responses are more likely when community acclimation lags behind the pace of warming (larger λ), when community composition is far from equilibrium before the onset of change (larger $|C(0)-E_0|$), and when the effect of community-climate disequilibrium on ecosystem function is large relative to direct climate sensitivity (larger γ, smaller β) (Section S2.3: Appendix S1). Communities acclimated to warmer-than-ambient conditions ($E_0 > C(0)$) before the onset of climate change are more likely to exhibit non-monotonic responses in ecosystem function, as warming may cause a reversal in the direction of acclimation when temperatures surpass the community climate niche (at first $dE/dt < 0$; later $dE/dt > 0$). We found that these conditions were also most likely to cause non-monotonic responses when the climate variable decreased rather than increased over time (Sections S2.2, S2.4, S3.2 and S3.4: Appendix S1).

We found that non-monotonic responses can have quadratic-like trajectories (e.g., initial decrease followed by a long-term increase; Figure 2c) or more complex cubic-like and quartic-like trajectories (Section S3: Appendix S1). Non-monotonic responses occur over the widest ranges of parameters when the effects of climate and community-climate disequilibrium on ecosystem function are multiplicative (e.g., $C(C-E)^2$ in Equation 3). Finally, the shape of climate sensitivity at equilibrium (Equation 2) can affect transient disequilibrium dynamics, but non-monotonic responses to climate change are likely regardless of the specifics of the equilibrium sensitivity. For forms of Equation (3) where the effect of climate on ecosystem function is exponentially saturating (Figures S2–S5, bottom rows), the conditions for non-monotonic dynamics are qualitatively similar compared to when equilibrium climate sensitivity is linear.

These results suggest that the contrasting initial and long-term responses of ecosystem function to warming observed in long-term experiments (Harte et al. 2015; Melillo et al. 2017; Reich

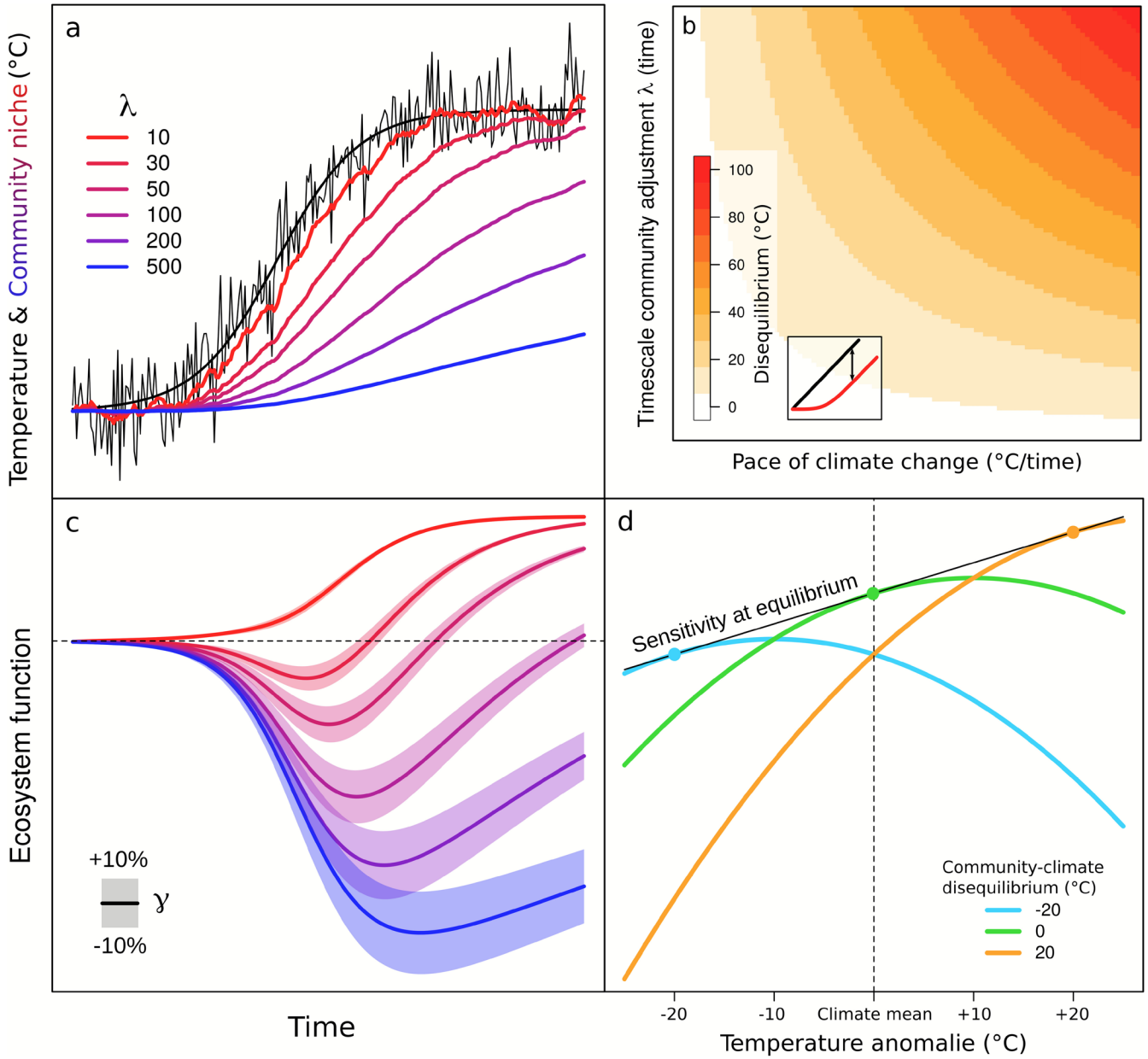

FIGURE 2 | Community-climate disequilibrium is a product of the pace of climate change and how quickly communities can acclimate. (a) Fast-acclimating communities (low λ, red curve) may keep pace with climate change and are responsive to interannual variation, but those that are slow to acclimate (high λ, blue curve) may experience growing disequilibrium. (b) If the pace of climate change is rapid, even communities that can acclimate quickly will experience disequilibrium (cell colours). For this illustration, community-climate disequilibrium was calculated as the difference between climate and community climate niche during a period of linearly changing climate (subpanel). (c) As climate shifts, slow-acclimating communities experience transient loss in ecosystem function even if the eventual equilibrium state is of increased function. Communities that acclimate quickly may never experience a transient loss of function. Ecosystem function is arbitrarily shown to increase in the long term, but the opposite pattern is possible if equilibrium climate sensitivity (β) is negative. As in panel a, each curve corresponds to a community with different λ values. Shaded bands represent a stronger or weaker effect of disequilibrium on function (γ). (d) Measured sensitivity of ecosystem function to climatic variation depends on community-climate disequilibrium. At a hypothetical site with temperatures varying interannually, a community acclimated to colder temperatures (blue curve) would lose function in warmer than average years, but a community acclimated to warmer temperatures (orange curve) would gain function in warmer-than-average years. Points and the sloping black line represent maximum functioning at a given temperature ($C = E$, Equation 2). In this arbitrary example, equilibrium climate sensitivity (β, black line) is positive, but negative relationships between climate variables and ecosystem function are equally possible.

et al. 2018; Reich and Hobbie 2013) may represent likely outcomes rather than unusual surprises. If non-monotonic ecological responses to monotonic climate change are pervasive, as indicated by the experiments and our analysis, then short-term observations will typically fail to predict long-term responses. Fortunately, our approach offers a tractable approach to forecast complex, transient dynamics by quantifying a few key parameters (λ, γ and E_0) (see Section 5).

4 | Can We Infer Community-Climate Disequilibrium From Ecosystem Function Time Series?

Whenever community-climate disequilibrium impacts ecosystem functioning, we need accurate measures of disequilibria, but quantifying community climate niches from species occurrence or abundance data are problematic. Current approaches for quantifying community climate niches (e.g., CTI & CPI) share the same assumptions as species distribution models (SDMs), where a species' biogeographic range is assumed to be representative of its climatic niche (Blonder et al. 2015; Devictor et al. 2008). These methods inherit the limitations of SDMs because they rely on occurrence data (but see Lalechère, Lenoir, et al. 2025; Lalechère, Marrec, and Lenoir 2025 for a non-equilibrium SDM approach). Most SDMs lose predictive power following rapid climate shifts (Zurell et al. 2009) because they ignore ecological lags (Essl et al. 2023). Range shifts are limited by dispersal distance (Corlett and Westcott 2013), geographic barriers to migration (e.g., bodies of water) (Davis et al. 1986), and slow soil development that hinders plant establishment (Pennington 1986). For these reasons, communities may often be out of equilibrium with climate, even during periods of relative climate stationarity (Seliger et al. 2021; Svenning et al. 2015). Lags aside, measures of the community climate niche might be biased due to asymmetric species climate response curves (Bonachela et al. 2021). Moreover, estimates of realised climate niches might not be transferable into the future due to non-analog climates and novel species interactions (Williams and Jackson 2007). Fundamental niches might be more reliable for this purpose, but are very difficult to measure in practice.

Assuming equilibrium when quantifying community climate niches is particularly problematic when disequilibrium and ecosystem function are the objects of research. Equation (1) emphasises that the rate of community climate niche change is determined both by the timescale of community acclimation (λ) and by the magnitude of community-climate disequilibrium. Lacking other knowledge, we cannot distinguish whether a rapid change in community composition is attributable to inherently fast community acclimation or to high initial disequilibrium. Further, community climate indices may be poor predictors of ecosystem function because they average across realised rather than fundamental climate niches.

Linking community-climate disequilibrium to ecosystem function (Equation 3) offers an alternative approach to study disequilibrium dynamics without directly measuring species' climate niches. By treating the community climate niche E as a latent variable, we can estimate the relevant parameters and infer disequilibrium over time using only ecosystem function and climate time series (see mathematical demonstration in Section S4.1: Appendix S1). Using this approach, ecosystem function F at a time t can be represented generally as

$$F(t) = h(C(t), C(t-1), F(t-1)), \tag{4}$$

where the function h depends on climate C at t, autoregressive terms for ecosystem function and climate, and the parameters λ, γ, α, β and E_0 from Equations (1) and (3) (full equation provided in Section S4.1: Appendix S1). Critically, h does not depend on $E(t)$, indicating the community climate niche is inferrable. The autoregressive terms ($C(t-1)$ & $F(t-1)$) are included to compare instantaneous rates of change in C and F, not as independent time-lagged predictors as would be the case when studying ecological 'memory' (Ogle et al. 2015). Treating E as a latent variable requires the assumption that the rate of community change is proportional to the magnitude of community-climate disequilibrium. However, we do not assume that systems start in equilibrium, or that there is a set timescale of community acclimation: E_0 and λ are free parameters. This approach adds a tool for estimating community climate niches when direct observations of community composition are absent or questionable but ecosystem function data such as remotely-sensed primary productivity are available (Robinson et al. 2018). Comparing results from the latent variable approach to those from established methods may be ecologically informative.

5 | Application to Simulated Metacommunity Data

Our approach is highly phenomenological, abstracting the joint effects of species' physiological plasticity, dispersal, competition, and numerous other processes that shape the pace of community acclimation. Can it predict community niche acclimation and reproduce transient dynamics in ecosystem function resulting from the collective action of community assembly processes? In this section, we provide a proof of concept by (1) generating a time series of ecosystem function using a metacommunity simulation, (2) fitting our acclimation model to the time series data using the latent variable approach described in the previous section and (3) evaluating the ability of our model to infer disequilibrium dynamics and predict functioning at the community level. To generate time series data, we used a relatively mechanistic plant metacommunity simulation (adapted from Alexander et al. 2018) in which species ranges respond to climate forcing, interspecific competition, intraspecific competition, dispersal and stochasticity. This simulation represents a hypothetical linear, one-dimensional series of sites along an elevation and temperature gradient. Although many climate variables vary along real-world elevation gradients, we focus on temperature for simplicity. Community composition differs along the gradient due to variation in species' thermal optima; coexistence is possible because intraspecific competition is stronger than interspecific competition, and communities are linked to neighbouring sites by dispersal (see Section S1: Appendix S1 for equations and a full description). There are no explicit time-delays in the simulation, but lags in community turnover emerge due to limited dispersal across sites, potentially unsuitable immigrant pools in neighbouring sites, and the slow buildup and decline of populations within sites. We represent overall ecosystem function within a site as the summed abundances of all species at that site, which we call 'community biomass'.

We focused on the response to warming of community composition and ecosystem function at one focal site in the middle of the warm half of the gradient. After allowing the metacommunity to equilibrate during a burn-in and initial stationary temperature period, we increased temperature by 3°C across 100 time steps at all 20 sites and tracked community responses for the following 5000 steps (Figure 3a). Specifics of the simulation were chosen

arbitrarily, and the temporal range was selected to show the extent of the resulting dynamics. Immediately following warming, species that are better suited to colder temperatures declined rapidly (Figure 3b, blue lines), and previously dominant species began to decline immediately or after a transient period of increase (Figure 3b, green lines). Resident species with warmer temperature optima increased in abundance, and newly competitive warm-adapted immigrants established slowly, benefitting from the decline of previous residents (Figure 3b, orange lines). These community shifts caused complex, transient dynamics in ecosystem function: community biomass first declined rapidly before recovering and gradually approaching a new equilibrium above the previous baseline (Figure 3c). The lag in community acclimation was evidenced by a slow change over time in the temperature at which community biomass growth rate is maximised (Figure 3d). Community biomass grew suboptimally for many time steps (pink points) before arriving at a new equilibrium (blue points).

To demonstrate the potential of our community-level approach for predicting transient dynamics and inferring community-climate disequilibrium, we fit our acclimation model (Equation 4) to the simulated time series of climate ($C(t)$) and ecosystem function ($F(t)$). We estimated the climate sensitivity (γ, α and β) and acclimation parameters (λ, E_0), and inferred community climate niche dynamics ($E(t)$). Critically, to test the ability of our model to infer disequilibrium, we withheld any information about species or community climate niches. For full methodological detail and to reproduce this analysis, see the accompanying code release (Stemkovski 2025).

Our model reproduced the initial decrease in community biomass, the subsequent recovery, and then the approach to a new equilibrium (Figure 3c, dashed line; $R^2 = 0.93$). We found that the transient dynamics resulted from slow community acclimation ($\lambda \approx 1000$ time-steps); there was a negative effect of community-climate disequilibrium on ecosystem functioning ($\gamma > 0$), and the equilibrium climate sensitivity of ecosystem function was positive ($\beta > 0$). We also found that there was little pre-existing disequilibrium ($E_0 \approx C(t = 1)$), which matched expectations because the simulation was allowed to equilibrate before the start of observation. Our acclimation model did not reproduce ecosystem function dynamics perfectly, slightly overestimating the magnitude of transient biomass loss. This may be because Equation (1) represents the dynamics of the centroid of the community climate niche rather than the whole distribution. In reality, individuals and species (and therefore communities) have some breadth in their climate niches, so initial responses to climate change may not be as drastic as Equation (1) would predict (Rodríguez-Sánchez et al. 2012).

The community climate niche (E) and its lagging acclimation are emergent properties of the metacommunity simulation, and we did not provide the acclimation model with any information about species composition. Nevertheless, the inferred trajectory of E correlated tightly ($r > 0.95$) with the observed community climate niche, measured as abundance-weighted averages of either species' fundamental temperature optima or the realised niche centroids, based on species' distributions before the onset of climate change (Figure 3e). This finding indicates that studying time series of ecosystem function could bolster inference about community climate niches and disequilibria. It also suggests that either the realised, fundamental, or inferred community climate niche would work for the purpose of capturing the dynamics of ecosystem functioning.

We note that climate, species niches and community biomass are closely linked in the metacommunity simulation. Might inference about the timescale of community acclimation and the effect of disequilibrium be different if we had studied a different ecosystem function? In real-world communities, other processes such as physiological acclimation and evolution also drive disequilibrium dynamics (Stemkovski et al. 2025). If the temporal grain of the data were fine enough to capture fast-acting processes, application of the latent variable approach to an ecosystem function that is more closely tied to ecophysiology than community composition might yield a lower estimate of λ and different γ, α and β coefficients. Characterising the dynamics of multiple interacting ecological acclimation processes is an open area of research (see Section 6.5).

Our community acclimation model captured the emergent transient dynamics caused by species interactions and dispersal lags, but why do we not incorporate these mechanisms into the acclimation model? While explicitly modelling community assembly processes to predict the effect of climate change on ecosystem functioning is appealing, the kind of metacommunity simulation model that we used to simulate data are not suited to empirical applications. Measuring the intra- and interspecific density dependence, climate optimum and niche breadth and dispersal rate of every species in most real-world regional species pools would be intractable. Even if we assume that pairwise interspecific interaction strengths are equal for all species, fitting this simulation model to a metacommunity of 50 species would require estimating 300 parameters, each of which would be difficult to measure in nature. Modelling disequilibrium at the community level by synthesising the mechanistic nuances of species interactions and dispersal using a handful of parameters offers a more parsimonious way to predict the effects of climate change on ecosystem function. This approach is similar in concept to functional-trait based methods (e.g., Chalmandrier et al. 2021), but we reduce complexity further by modelling at the level of the whole community.

6 | Future Research Priorities

Predicting the impact of climate change on ecosystem functioning across different timescales will require models capable of representing complex, transient dynamics but simple and general enough to fit with common data sources. Our approach attempts to strike this balance by linking community-climate disequilibrium to ecosystem functioning with minimal parameters. Beyond helping to make accurate predictions, our framework suggests novel hypotheses related to each of the three critical parameters: the community acclimation timescale (λ), pre-existing community-climate disequilibrium (E_0) and the sensitivity of ecosystem function to disequilibrium (γ). The following research agenda focuses on testing these hypotheses to advance understanding of ecological responses to climate change.

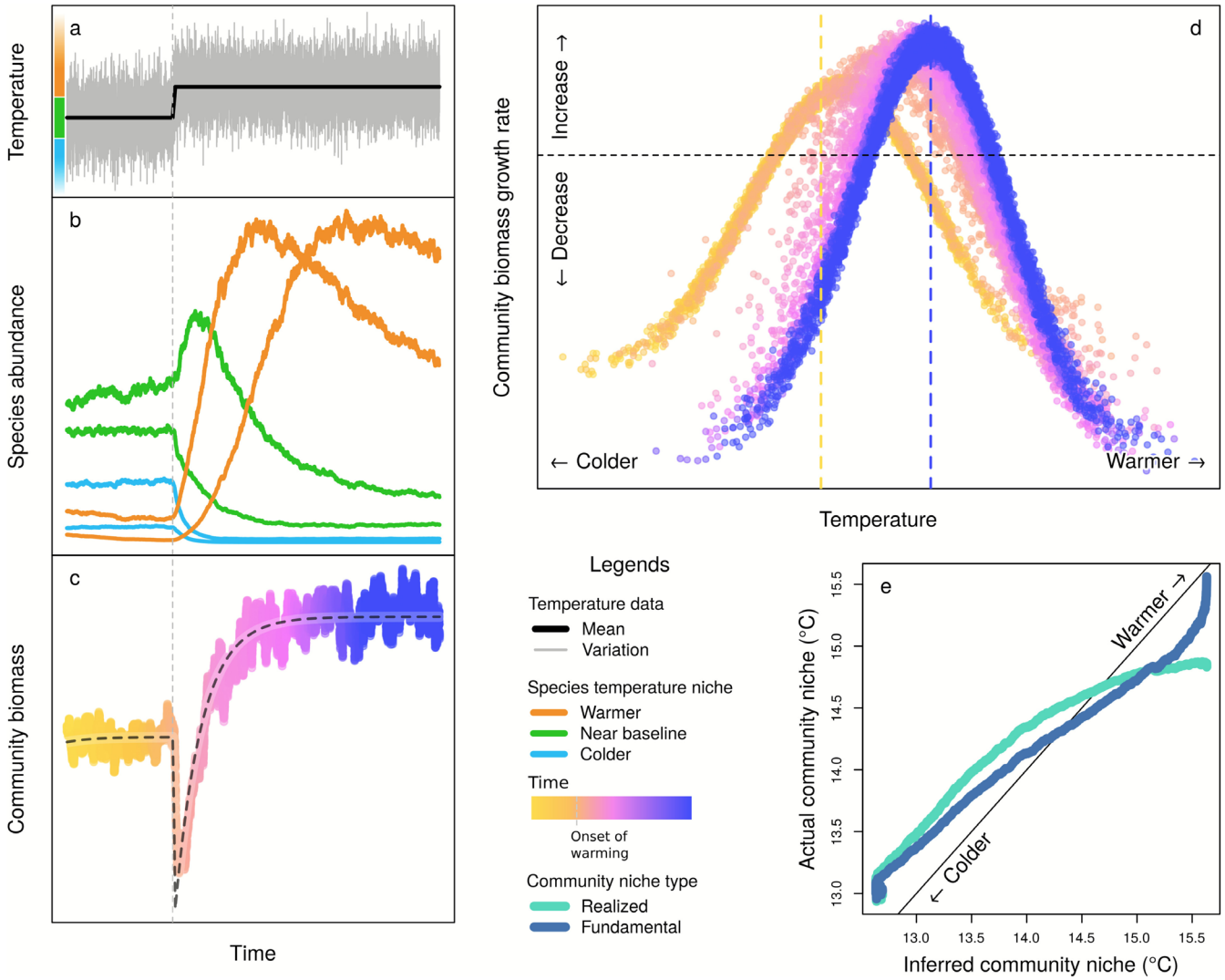

FIGURE 3 | A simulated plant community exhibits complex transient dynamics of ecosystem function in response to warming. (a) The temperature at each time step (grey lines) varies around the mean temperature (black line). Horizontal coloured lines correspond to species temperature niches. (b) Blue, green and orange curves show species abundance changes over time for a subset of the community at a focal site. The line colours correspond to species' fundamental temperature niche optima relative to pre-warming temperature ranges shown in panel a. (c) Community biomass (the sum of all species abundances at the focal site: A proxy for ecosystem function) transiently decreased in response to warming. Colours correspond to time from the start of the simulation. When fitted to the simulated temperature and biomass time series, the system of Equations (1) and (3) captured the community biomass dynamics (black dashed curve). (d) The transient loss of biomass was caused by slow community acclimation. Each point represents the change in community biomass in a time step, and points below and above the horizontal dashed line indicate a decrease and increase in biomass, respectively. Vertical lines show the mean temperature before and after warming. (e) Though the acclimation model was not given any direct information about community composition, it was able to infer community climate niche dynamics as represented by realised (teal line) and fundamental (blue line) community climate indices.

6.1 | Measure Community Acclimation Timescales and Their Predictors

Understanding acclimation timescales is critical for predicting whether climate change will increase community-climate disequilibria and impact ecosystem functioning. Many studies have measured factors that influence acclimation timescales, but knowledge is fragmented across ecosystems, processes and ecological subdisciplines. A focus on acclimation timescales can synthesise this knowledge. We hypothesise that *community acclimation timescales decrease with habitat connectivity, dispersal rates, and the richness of regional species pools, but increase with organismal generation times and competition during establishment* (Alexander et al. 2018; Bektaş et al. 2024; Bertrand et al. 2011; Fredston et al. 2024). Partitioning the effects of multiple determinants of community-climate disequilibria can be particularly informative (Bertrand et al. 2016), and related frameworks such as ecological 'memory' and 'legacies' could provide estimates of acclimation timescales, especially for relatively fast processes (Anderegg et al. 2015; Ogle et al. 2015). Quantifying community acclimation timescales will help us to compare disequilibrium dynamics across systems (Bertrand 2019; Svenning and Sandel 2013), forecast across a wide range of time horizons (Adler et al. 2020), and

inform anticipatory natural resource management (Bradford et al. 2018; Lynch et al. 2022). Understanding which communities are slowest to acclimate can inform efforts such as assisted migration that seek to maintain ecosystem functions (Hällfors et al. 2017). Using long-term species composition and climate time series data (Dornelas et al. 2025) is perhaps the most promising path for estimating acclimation timescales, but, as we have shown, acclimation timescales could also be inferred from time series on climate and ecosystem functioning.

We caution that acclimation timescale (λ) only represents the capacity of communities to respond to climate change: Equation (1) shows that observed rates of community acclimation (dE/dt) may also be greater in places where climate change exacerbates pre-existing community-climate disequilibrium (E_0). For this reason, studies measuring acclimation timescales and their predictors should not assume that communities were in equilibrium before recent climate change. In other words, the degree of current extirpation debt ($C - E_0$ opposes the direction of dC/dt) or immigration credit ($C - E_0$ matches the direction of dC/dt) in a community is likely to influence its response to climate change (Jackson and Sax 2010).

6.2 | Utilise Spatial Variation in Current Community-Climate Disequilibrium

Focusing on community-climate disequilibria that already exist in communities can help us better understand the current functioning of communities and anticipate their sensitivity to increasing disequilibrium in the future. Many studies have compared community climate niches across systems and tracked their change through time, but few, if any, have used this information to explain ecosystem functioning. We predict that *differences in pre-existing community-climate disequilibria (E_0) across geographic regions can explain spatial variation in ecosystem functions that is not explained by climate*. Communities are rarely in equilibrium with climate due to factors such as source-sink dynamics, historical contingency and disturbance (Blonder et al. 2015; Devictor et al. 2012; Perez-Navarro et al. 2022; Rosenblad et al. 2023), but studies of ecosystem function across spatial climate gradients typically ignore variation in the magnitude of disequilibrium across communities. Our framework suggests that communities that are in equilibrium with climate may function differently than those that are out of equilibrium (Figure 2d). Specifically, we might observe opposite patterns of climate sensitivity depending on whether disequilibrium is positive or negative. A community that is acclimated to wet conditions might show decreased function in dry years, but another community subject to the same climate might show increased function in dry years if it is acclimated to even drier conditions.

To test this prediction empirically, we propose quantifying disequilibrium across communities by first comparing climate averages (mean annual temperature and precipitation) to community climate niche metrics such as CTI and CPI. Such occurrence-based measures of community climate niches rely on equilibrium assumptions at the species level (see Section 4), but they offer tractable ways to relax equilibrium assumptions at the community level. Second, the resulting estimate of disequilibrium can be used as a predictor of the sensitivity of an ecosystem function to temporal climatic variation (Equation 3). The key question is whether information about disequilibrium helps explain variation in ecosystem functioning across space or in response to temporal climate variation. This approach could be applied to any existing dataset in which species composition and ecosystem function are recorded in multiple locations, such as forest inventory and dendrochronological growth rate data (Peltier et al. 2022; Tinkham et al. 2018). Such an analysis would benefit from more precise and accurate measures of community climate niches than default occurrence-based approaches. Methods that account for species interactions (e.g., Bertrand et al. 2011; Liu et al. 2020) could help reduce bias in CTI and CPI calculations, as interactions can influence both species' realised niches and ecosystem functions.

6.3 | Predict the Sensitivity of Ecosystem Function to Community-Climate Disequilibrium

Our findings suggest that communities whose functioning is strongly affected by community-climate disequilibrium are more likely to exhibit complex responses to climate change such as reversals in climate sensitivity over time (Figure 3c; Section 4). We hypothesise that *the effect of disequilibrium (γ) is strongest in communities of species with narrow climate niches and low variation across species' climate niche optima*. Until now we have focused on the central tendency of community climate niches (E), but this hypothesis focuses on the relationship between the breadth of the community climate niche and the effect of disequilibrium on function. In our model, the parameter γ controls the steepness of the loss in function as climate departs from a community's optimum (Figure 3d), analogous to the breadth of species-level thermal performance curves (Rezende and Bozinovic 2019). Climate niche breadths are likely to be greater in communities dominated by species with high and reversible trait plasticity (Carscadden et al. 2020; Valladares et al. 2014), and we expect the effect of disequilibrium to be weaker in such communities. Plasticity evolves in climates that fluctuate predictably at timescales comparable to species generation times (Botero et al. 2015), so knowledge about ancestral climate regimes may help explain present-day community sensitivities to disequilibrium. At the community level, climate niche breadth should also increase with the dispersion of climate niche optima across species, and the shape of species climate response curves can influence acclimation timescales (Bonachela et al. 2021).

These hypotheses could be tested empirically by pairing data on species-level thermal performance curves with time series of ecosystem function for multiple communities. An ideal dataset would include in situ functioning at the species level, but large-scale analyses may have to rely on community-level data such as remotely-sensed primary productivity (Lian et al. 2020, 2021; Robinson et al. 2018). Metacommunity simulation experiments that vary climate niche patterns within and across species could provide initial tests of hypotheses about the functioning of real communities.

6.4 | Forecast Complex Ecosystem Function Dynamics at Intermediate Time Horizons

Our results emphasise that the sensitivity of an ecosystem function to climate change will shift over time as disequilibrium dynamics play out. However, many current forecasting approaches effectively ignore disequilibrium dynamics by making implicit assumptions about the pace of community acclimation. Forecasts based on spatial data such as species distribution models and space-for-time substitutions do not usually account for lagging processes (effectively assuming that E always matches C) (Essl et al. 2023; Evans et al. 2025), and forecasts based on short-term time series data treat community composition as stationary (effectively assuming that E is invariant) (Wolkovich et al. 2014). These assumptions are consequential: when forecasting ecosystem function, the choice of whether to base projections on spatial or temporal patterns can represent as much uncertainty as future greenhouse gas emission scenarios (Felton et al. 2022; Perret et al. 2024). Such differences between spatial and temporal measures of climate sensitivity are widespread across regions and taxa (Buechling et al. 2017; Gaüzère and Devictor 2021; Kleinhesselink and Adler 2018; Klesse et al. 2020; La Sorte et al. 2009; Miller et al. 2018; Oldfather et al. 2021). Forecasts based on the spatial relationship between temperature and ecosystem function may predict long-term patterns but perform poorly in the short-term, and those based on temporal comparisons do well in the short-term but make unrealistic long-term projections (Adler et al. 2020; Evans et al. 2025; Stemkovski et al. 2025). Neither approach is appropriate for the intermediate forecast horizons critical for managing climate adaptation and resilience (Bradford et al. 2018).

Our proposed framework has the potential to improve intermediate-term forecasts by explicitly modelling disequilibrium dynamics. Rather than assuming that community climate niches will remain stationary ($E(t) \approx E_0$, large λ) or that communities always track climate by acclimating rapidly ($E(t) \approx C(t)$, small λ), we should treat community acclimation as a dynamic process (Equation 1) that influences the functioning of communities (Equation 3).

6.5 | Extend Theory and Develop Statistical Tools

Testing the hypotheses described in the previous sections will require new theory and statistical tools that do not rely on equilibrium assumptions (Lalechère, Lenoir, et al. 2025). We have focused on climate-driven change in species composition, but other processes such as physiological acclimation, phenological shifts and evolutionary adaptation can also affect community-climate disequilibrium and influence ecosystem functioning (Stemkovski et al. 2025). New theory should focus on representing these processes simultaneously. The dynamics of these processes have been characterised by equations analogous to Equation (1) (Chevin et al. 2010; Friend 2010; Rezende and Bacigalupe 2015), suggesting that interacting components of ecological acclimation could be modelled with multiple iterations of Equation (1) or by treating the acclimation timescale (λ) as a distribution. When longitudinal data are available, methods developed to quantify 'ecological memory' with distributed lag-time kernels could help reach this goal (Ogle et al. 2015).

An open question is how these acclimation processes interact: just as plasticity may slow evolutionary adaptation (Price et al. 2003), will evolutionary adaptation slow compositional change and vice versa? Extending our latent variable approach may be useful for estimating overall structural disequilibrium resulting from many simultaneous ecological acclimation processes. Additionally, because communities acclimate to multiple dimensions of climate (Blonder et al. 2015), we need to examine community acclimation driven by simultaneous, potentially interacting forcings such as changes in both moisture and temperature.

We successfully fit our theoretical model to simulated data (Section 5), but empirical applications of the latent variable approach will be more difficult because the datasets will be smaller and noisier with a weaker signal. Before diving into empirical data, we need to explore the limits of statistical estimation. Open questions include parameter identifiability, the length and resolution of time series data needed to reliably infer community-climate disequilibrium, and the utility of interannual variation during periods of stationary climate for estimating acclimation timescales. Initial analysis indicates that γ, λ, α, β and E_0 are identifiable (Section S4.2: Appendix S1), but testing with more complex community responses is needed to ensure that inference is robust.

Finally, we would benefit from new methods for measuring community-climate niches without assuming that all species ranges are presently in equilibrium with climate (Lalechère, Marrec, and Lenoir 2025; Seliger et al. 2021). Treating community-climate disequilibrium as a latent variable and estimating E_0 using climate and ecosystem function time series is a novel alternative to current methods for calculating community-climate niches based on species distribution data and relative abundances (Blonder et al. 2015; Devictor et al. 2008; Essl et al. 2023; Zhu et al. 2012). We do not envision this approach replacing direct estimates of community climate niches, but using large-scale measures of ecosystem function such as remotely-sensed primary productivity datasets (Robinson et al. 2018) has the potential to expand the scope of community-climate disequilibrium studies.

7 | Conclusion

Many ecological communities are unlikely to respond to climate change rapidly enough to maintain historical levels of ecosystem function. To understand and predict the consequences of lagging community acclimation, it is helpful to think about community-climate disequilibrium as a dynamic quantity that influences the relationship between ecosystem function and the climate. We have presented a theoretical model that makes this conceptual link and that is general enough to be applied across different environments and communities. We hope that this model promotes the adoption of disequilibrium concepts by researchers, opens new lines of inquiry that utilise community climate niches, and leads to more accurate and useful forecasts of ecosystem responses to climate change.

Author Contributions

M.S., J.B.B., A.J.L., C.R.R. and P.B.A. conceived the study and managed the project. M.S. wrote primary drafts. M.S. and P.B.A. developed the model. M.S. and M.H.C. designed and performed mathematical analysis. M.S. and K.B. performed statistical analysis and visualisation. J.R.B., K.C.-W., M.H.C., M.E.K.E., L.C.J., M.A.P., M.L.P., O.S., A.P.W. and J.W.W. refined ideas for the model. All authors edited drafts.

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Data Availability Statement

All code and data are publicly available through Zenodo at https://doi.org/10.5281/zenodo.17784117. Additionally, users can explore the theoretical model equations through an interactive R-Shiny app at https://www.stemkovski.com/visualizations/ecological-acclimation-app.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Forms of the equation relating disequilibrium to ecosystem function. **Table S2:** Discontinuous and continuous changes in each term in equation (S3) in response to an instantaneous increase in climate. **Table S3:** Discontinuous and continuous changes in each term in equation (S3) in response to an instantaneous decrease in climate. **Table S4:** Predicted responses of each term in form (S3) to a linear increase in climate. **Table S5:** Predicted responses of each term in form (S3) to a linear decrease in climate. **Figure S1:** Illustrations of the temporal dynamics of each term in equation (S3) in response to a linearly increasing climate, $C(t) = C_0 + rt$. **Figure S2:** Illustrations of the temporal dynamics of each term in equation (S3) in response to a linearly decreasing climate, $C(t) = C_0 - rt$. **Figure S3:** Ecosystem function responses to a linearly increasing climate for (row 1) the linear dependence form and (row 2) the nonlinear dependence form of $F_2 = \alpha + \beta g(C) - \gamma C\Delta^2$. **Figure S4:** Ecosystem function responses to a linearly increasing climate for (a) $F = \alpha + \beta C - \gamma\Delta^2$, (d) $F_3 = \alpha + \beta[1 - \exp(\kappa C)] - \gamma\Delta^2$ and (b, c) $F_4 = \alpha + \eta E - \gamma\Delta^2$. **Figure S5:** Ecosystem function responses to a linearly increasing climate for (row 1) the linear dependence form and (row 2) the nonlinear dependence form of $F_5 = \alpha + \beta g(C) + \eta E - \gamma C\Delta^2$. **Figure S6:** Ecosystem function responses to a linearly increasing climate for (row 1) the linear dependence forms and (row 2) the nonlinear dependence forms of (column 1) $F_6 = \alpha + \beta g(C)/[1 + \gamma\Delta^2]$ and (column 2) $F_7 = (\alpha + \beta g(C))\ \exp(-\gamma\Delta^2)$. **Figure S7:** Ecosystem function responses to a linearly decreasing climate, $C(t) = C_0 - rt$. **Figure S8:** Community-climate niche dynamics can be inferred by treating it as a latent variable that is related to climate and ecosystem function time series data. **Figure S9:** Identifiability of the five parameters estimated by the latent variable model.