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Predicting and controlling ecological communities via trait and environment mediated parameterizations of dynamical models

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Predicting or controlling the state of an ecological community is a core global change challenge. Dynamical models provide one toolkit, but parameterizing these models can be challenging, and interpretation can be difficult. We here propose rewriting dynamical model parameters in terms of more interpretable and measurable functional traits and environmental variables (trait and environment mediated parameterizations; TEMPs). For prediction, this approach could help make interpretable forecasts of equilibrium community dynamics (species coexistence), invasibility surfaces (dynamics due to biotic context), and responses to environmental change (dynamics due to abiotic context). For control, this approach could help identify policies that yield desired species and trait compositions through perturbations of the abundance of species with certain traits, or of the environment.

Keywords: community dynamics, prediction, optimal control, dynamical model, forecast, functional trait

Introduction

Many contemporary challenges facing human societies are linked to predicting or controlling the dynamics of ecological communities. These ecological problems are linked to a wide variety of cases including managing pests to maintain crop yields (Thomas 1999), restoring or stabilizing ecosystems to historical baselines (Palmer et al. 1997), or improving human health through the manipulation of our microbiome (Sonnenburg

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2015, Widder et al. 2016) and disease vectors (Johnson et al. 2015) like malaria (Ferguson et al. 2010). Conceptual advances around prediction or control may then improve our ability to address these challenges with ecological theory.

Prediction and control of communities are closely linked (Fig. 1; see Box 1 for terminology). Prediction asks: 'given that the community is in state A, and some (or no) perturbations occur, does it then reach state B, C, or D, and by which trajectory?'. The end state is unknown in advance, but the community will follow one trajectory to reach it. The challenge is to select from a large or infinite number of potential trajectories. In contrast, control asks: 'given that the community is in state A, how can we optimally ensure it reaches the desired state B, potentially along a particular trajectory?' Here, the end state is specified, and the emphasis is on identifying which trajectory brings the community to that state and at what 'cost'. The challenge is to select from the large or infinite number of possible trajectories that reach the specified end state. In the prediction problem, few, or zero, perturbations are considered; in the optimal control problem, a potentially infinite number of perturbations are considered in a sequence that drives the dynamics. Broadly, useful predictions are a prerequisite for useful control, because in control one needs to predict the consequences of any given perturbation on a community.

We focus on these challenges in dynamical models because they are widely used for community ecology. Dynamical models include relatively simple analytic models such as the generalized Lotka–Volterra (GLV) model (Chesson 2000, Barabás et al. 2016, Grilli et al. 2017, Serván et al. 2018), as well as more complex simulation models such as the SORTIE-ND forest dynamics model (Pacala et al. 1996) or the COMETS microbial dynamic flux balance model (Dukovski et al. 2021).

We identify four key concerns relevant to prediction and control for dynamical models. First, dynamical models often have large numbers of parameters that scale super-linearly with the number of species considered (e.g. a matrix of interaction coefficients). The parameter space dimensionality problem can make it difficult to parameterize a model (e.g. Godoy and Levine (2014) who carried out numerous pairwise competition experiments to parameterize a dynamical model). Second, these parameters can sometimes be difficult to biologically interpret. For example, in the GLV model, the interaction coefficient parameters define per capita demographic effects of one species on another, which may not be as straightforward to interpret as a trait (e.g. Vucic-Pestic et al. (2010) who reduced parameter space dimensionality using a body mass trait). Third, these parameters may not be constant in time, and may change with environmental conditions. This variability implicitly requires re-measurement across environments, or decreased confidence in model extrapolations to new environments (e.g. Pennekamp et al. (2018) who carried out protist competition experiments at multiple growth temperatures). And fourth, from a control perspective, some of these parameters are difficult to imagine perturbing, while state variables like abundance or the environment are more easy to imagine perturbing (e.g. Angulo et al. (2019) who propose perturbing abundances instead of interaction coefficients). For example, it may not be possible to perturb *only* the per capita impact of species 1 on species 2 without also causing unpredictable perturbations to other model parameters; or it might not even be clear how such a complex parameter could be perturbed.

Here, we propose an alternate approach, trait-environment mediated parameterization ('TEMP'). In TEMP, functional trait and environment variables influence communities at the level of dynamical model parameters (e.g. determining

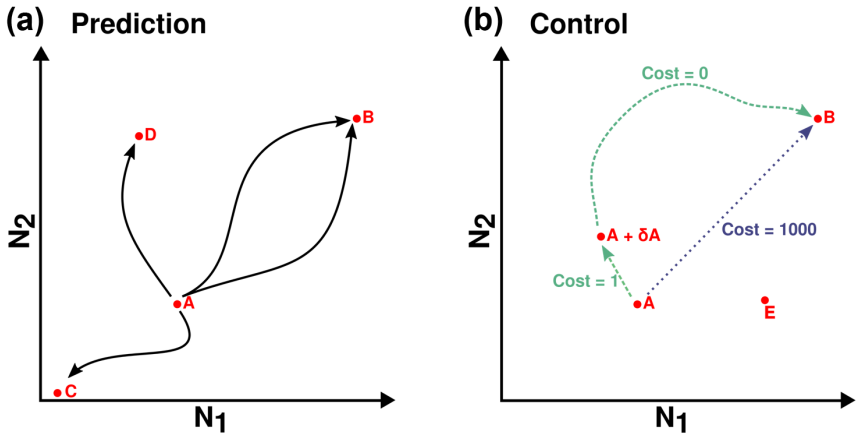

Figure 1. Illustration of concepts for predicting or controlling the state of a community. Consider a state space of two species' abundances, N_1 and N_2 along the axes and an initial state (A). (a) Predictability measures our ability to know the community's future state. In this example, the community at state A could transition to several future states (B, C, or D) through one or more trajectories each. (b) Controllability reflects the possibility of reaching a desired state (here, B, with high abundance of species 1 and species 2). Directly shifting the community to the desired state (purple arrow) may require a high-cost perturbation (either high effort or long time), but one could instead identify a lower cost indirect perturbation (δA, green dashed arrow) to state A + δA. After this perturbation, the community will reach state B at minimal additional cost. In contrast, no perturbation can reach state E, which is then considered unreachable (infinite cost).

Box 1. Glossary.

Action - a perturbation that we can choose to make to one or more of the state variables.
Controllable - the degree to which a system can be shifted its present state to a desired state within a specific time frame through actions.
Control policy - a specific set of actions that we could implement to achieve a desired state.
Desired state - the values of the state variables that we wish the community to reach after some amount of time.
Optimal – a term used to describe a control policy that minimizes or maximizes some criteria. For example, we could reduce the abundance of an invasive species by taking the action of manipulating the environment to be unsuitable (i.e. high cost, high effort, low chance of off-target effects), or take the action of manipulating the abundance of a natural enemy at key time points when the population of the invasive species is most sensitive (i.e. low cost, low effort, potential for off-target effects).
Perturbation – an external change to a state variable of a system. Here perturbations are considered with respect to the abundances of species with certain traits or the environment. A perturbation may occur continuously over time or impulsively.
Predictable - the potential for making accurate predictions about a system. High predictability means that the future state of the system can be more readily determined.
Prediction – a specific, quantitative, and falsifiable statement about the future state of a system.
Reachable - the potential for obtaining a certain state in the future, given a dynamical model and a current state, and any perturbations applied via a control policy. Not all desired states are necessarily reachable.
State variable - a variable that describes the current state of the system. Examples include the abundances of the species that are present in (or absent from) the community and the environment.

competitive interactions in the GLV model), rather than at the level of community properties. While the underlying prediction and control problems are still naturally defined in terms of their state variables (abundances) and dynamical model parameters, rewriting those parameters in terms of trait and environment variables may provide a useful 'middleman' step. For prediction problems, TEMP enables reformulation in terms of measurable and interpretable trait or environment variables. For control problems, TEMP provides realistic leverage points for control problems via identifying species with certain traits or certain environments which can then have their abundances perturbed, or for reaching certain trait distribution targets as the outcome of control. Previous efforts to reduce dynamical model parameter set dimensionality have been limited to environment parameterizations (Lanuza et al. 2018, Maynard et al. 2020) or trait parameterizations (Vucic-Pestic et al. 2010) alone, and have not explored further interactive consequences for prediction and control problems.

There is a long history of using trait and environmental variables in community ecology (Gaudet and Keddy 1988, Keddy 1990, Lavorel and Garnier 2002, Violle et al. 2007). Examples include measuring community-level properties like trait dispersion patterns (Kraft and Ackerly 2010, Mayfield and Levine 2010, HilleRisLambers et al. 2012), predicting abundances (Shipley et al. 2006, Laughlin et al. 2012), or explaining processes related to species fitness (Laughlin et al. 2020) and coexistence (Angert et al. 2009, Kraft et al. 2015, Kunstler et al. 2016). However, leveraging models to predict or control the future of a community beyond mechanistic explanation or pattern description has been less explored. TEMP thus build on recent calls to integrate functional traits with demography (Webb et al. 2010, Salguero-Gómez et al. 2018, Laughlin et al. 2020, Chalmandrier et al. 2021) and to leverage traits for restoration and design-related problems in applied ecology (Widder et al. 2016, Wainwright et al. 2018). It also builds on existing trait-focused methods for prediction (Laughlin et al. 2012, Laughlin and Messier 2015, Warton et al. 2015, Li et al. 2021) and control (Laughlin 2014a, Giannini et al. 2017, Laughlin et al. 2018, Clark et al. 2021, Baranwal et al. 2022) by linking community ecology and traits at the level of dynamical model parameters.

Here, we outline how dynamical models can be parameterized via TEMP (part 1). This then allows common prediction problems to be framed in terms of trait or environment variables (part 2). In turn, this allows common control problems to be addressed by identifying abundance perturbations to species with certain traits or to environment variables that differentially impact the abundance of species with certain traits (part 3). Because our goal primarily is to introduce concepts, we focus on two representative implementations of TEMP within the well-known generalized Lotka–Volterra dynamical model. The same approach could be taken for any other dynamical model when some of its parameters can be rewritten using TEMP.

Part 1. Trait and environment mediated parameterizations for dynamical models

The TEMP approach addresses the four key concerns relevant to prediction and control described above. First, in TEMP, parameters can be treated as non-independent from one another because species with similar functional trait values or in similar environmental contexts should have similar responses, e.g. as in trait-based dynamic global vegetation

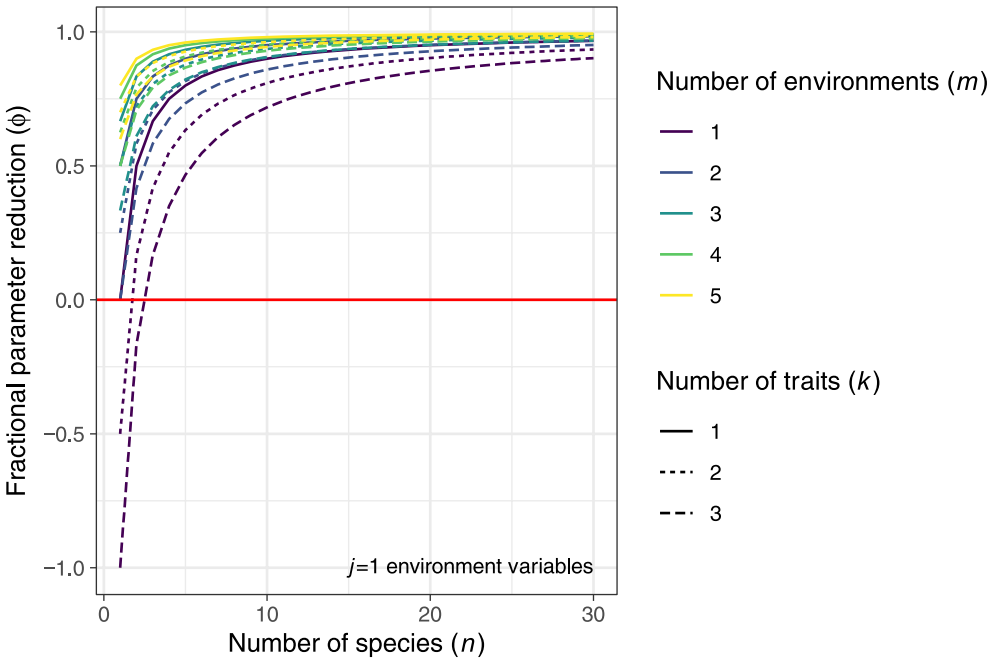

Figure 2. TEMP can sometimes reduce parameter estimation challenges in the GLV model. In the GLV model of n species parameterized in each of m discrete conditions, there are $m\left(n^2+n\right)$ free parameters to estimate. Alternatively with the TEMP described in Box 2, if k traits characterize each species, and j environmental variables can describe the conditions, then there are instead $j+nk$ free parameters to estimate. The fractional reduction in number of parameters to be estimated, is then $\phi=1-\left(j+nk\right)/\left(m\left(n^2+n\right)\right)$. This ratio is small when $k+j/n \ll mn$, or when the number of traits and environmental parameters is smaller than the product of the number of species and conditions. In the simplest case where there is no environmental variation, this reduces to $k \ll n$, i.e. a large reduction in parameters when the number of traits is much smaller than the number of species. Note that more complex TEMP or dynamical models might not yield similar fractional reductions.

models (van Bodegom et al. 2014). This non-independence drives correlations in model parameters and can, for some dynamical models and TEMP choices, reduce the effective number of variables that need to be independently estimated (Fig. 2). Second, TEMP facilitates interpretation of community-level properties like competition or coexistence in terms of measurable functional traits, like body mass differences between species. Third, TEMP inherently accounts for how dynamical model parameters change with the environment. And fourth, TEMP helps move beyond the high dimensionality of control problems and the intractability of perturbing individual parameters. TEMP can identify environment variables that can be perturbed to cause shifts in the underlying dynamical model parameters, and also can identify species with certain traits whose abundance could be usefully perturbed.

Here we illustrate the TEMP approach within the generalized Lotka Volterra (GLV) model. This model is widely used in theoretical community ecology (Barabás et al. 2016, Grilli et al. 2017, Saavedra et al. 2017, Angulo et al. 2021) and also for empirically describing communities (Buffie et al. 2012, Stein et al. 2013, Coyte et al. 2015, Venturelli et al. 2018). It is also closely linked to the Beverton-Holt model for discrete-time community dynamics (Beverton 1957) and its annual plant-seedbank derivatives (Venable et al. 1993, Godoy and Levine 2014, Weiss-Lehman et al. 2022). The GLV model includes density-independent species growth (the r parameter) and density-dependent competition (intra- and inter-specific) (the A parameter). We summarize this model and illustrate coupling it to TEMP in Box 2. We then focus on illustrating several TEMPs that could be used within the GLV model. These are simple demonstration TEMPs; more complex ones would likely be needed for real applications.

For competition, we explore two representative biological processes. In a limiting similarity TEMP, species with different traits have more distinct niches, resulting in weaker interaction coefficient parameters (Macarthur and Levins 1967, Abrams 1975, Kraft et al. 2015). In a competitive hierarchy TEMP, a relatively higher trait value confers dominance over less extreme trait values (e.g. plant height in the context of light competition), resulting in hierarchically modular interaction coefficient parameters (Gaudet and Keddy 1988, Grime 2006, Violle et al. 2009, Mayfield and Levine 2010, Kunstler et al. 2012). Interaction coefficients also have been hypothesized to be environmentally dependent (Grime 1977, Goldberg and Barton 1992, Bimler et al. 2018, Lanuza et al. 2018, Matías et al. 2018), e.g. fewer negative interactions in more extreme environmental conditions (Maestre et al. 2009, Weiss-Lehman et al. 2022); a version of the 'stress gradient hypothesis').

Box 2. Demonstration implementation of TEMPs in the generalized Lotka– Volterra model.

Dynamical model

Consider a regional pool of *n* species, with abundance of species as N_i, such that the composition of the community at time t_1 is the vector $\vec{N}\left(t_1\right) = \left\{N_i\left(t_1\right)\right\}$. Suppose also that the environment is defined by a vector of variables, $\vec{E}\left(t_1\right) = \left\{E_k\left(t_1\right)\right\}$. The goal is to predict or control $\vec{N}\left(t_2\right)$ for $t_2 > t_1$. The generalized Lotka–Volterra model is a useful baseline because it accounts for density-dependent effects of species on themselves and other species. The vector of abundances $\vec{N}$ solves a linear system of differential equations:

$$\frac{d\vec{N}\left(t\right)}{dt} = diag\left(\vec{N}\left(t\right)\right)\left(\vec{r} + A\vec{N}\left(t\right)\right) \quad (1)$$

where $\vec{r}$ is the vector of density-independent growth rates, and ***A*** is the matrix of interaction coefficients, with entry A_{ij} representing the change in species *i*'s per capita growth rate for a unit change in the density of species *j*.

The trait-environment mediated parameterization (TEMP)

Eq. 1 parameters can be modeled by assuming links between trait and environment as:

$$A_{ij}\left(t\right) = f\left(\vec{T}_i, \vec{T}_j, \vec{E}\left(t\right)\right) \quad (2)$$

$$r_i\left(t\right) = g\left(\vec{T}_i, \vec{E}\left(t\right)\right) \quad (3)$$

Here, *i* and *j* index species, *f* and *g* are functions, $\vec{T}_i$ is a vector of trait values, and $\vec{E}$ is a vector of environmental variables. Equation 2 and 3 both incorporate potential temporal variation in ***A*** and $\vec{r}$ arising from temporal variation in the environment. We explore two TEMPs for Eq. 2:

$$\text{Limiting similarity TEMP: } A_{ij}(t) = \varphi\left(\vec{E}\left(t\right)\right)\times\left(-1 / \left|\vec{T}_i - \vec{T}_j\right|\right) \quad (4)$$

$$\text{Competitive hierarchy TEMP: } A_{ij}\left(t\right) = \varphi\left(\vec{E}\left(t\right)\right)\times If\left\{\vec{T}_i > \vec{T}_j, -\left(\vec{T}_i - \vec{T}_j\right)\right\} else\left\{0\right\} \quad (5)$$

where φ is a scaling function. In our examples, we use:

$$\varphi\left(\vec{E}\left(t\right)\right) = \left(1 + \left|\vec{E}\left(t\right)\right|\right)^{-1} \quad (6)$$

which represents a 'stress gradient' in which competitive interactions become stronger at lower values of the environment. TEMPs can be 'normalized' to high intraspecific competition, such that if $i = j$, then $A_{ij} = -1$; otherwise, for the off-diagonal entries, we divide them by the largest magnitude off-diagonal value. For the normalized limiting similarity TEMP, we also impose a threshold such that if $\left|\vec{T}_i - \vec{T}_j\right|$ is smaller than the 10% quantile of all pairwise values, it is set to the 10% quantile value. This threshold avoids numerical issues where A_{ij} may become unrealistically large for species with very similar trait values. In the control examples, we explore a non-normalized version of limiting similarity where off-diagonal entries are not normalized and a quantile threshold is not used, as this permits for stronger species interactions that can be leveraged for control.

We also assume a simple linear TEMP for intrinsic growth rate, i.e.

$$r_i\left(t\right) = \alpha \vec{T}_i \tag{7}$$

We chose a simple linear form (dependent on traits, no environment dependence) for illustrative purposes. Real TEMPs will likely be more complex and multivariate.

Prediction

Predictions of the future abundance of all species can be determined by numerically integrating $\frac{d\vec{N}\left(t\right)}{dt}$. In the GLV case, the fixed point can be found algebraically as (Serván et al. 2018):

$$N_i^* = -A_{ij}^{-1} \times r_i \tag{8}$$

Feasibility can be determined by assessing whether $N_i^* > 0$ for all species. Local stability can be determined by identifying whether perturbations are damped out near equilibria. In the GLV case, the fixed point can be found as:

$$\max\left(\mathrm{Re}\left(\{\lambda_i\}\right)\right) < 0 \tag{9}$$

where $\{\lambda_i\}$ are the eigenvalues of $diag\left(N_i^*\right)A$ (Barabás et al. 2016).

Short-term invasibility can be determined by assessing whether invader equilibrium abundance is non-negative, i.e.

$$\lim_{t\to\infty} N_i\left(t\right) > 0 \tag{10}$$

Calculated when $N_i(t)$ is introduced at near-0 abundance and when all other species are close to equilibrium abundance.

Trait–environment relationships and environmental change responses can be determined by defining $\mu\left(N_i\left(t\right), \vec{T}_i, \vec{E}\left(t\right)\right)$ as a community-scale summary statistic of species abundances and traits, then comparing $\mu\left(t\right)$ to $\vec{E}\left(t\right)$ (Gaüzère et al. 2020a).

For species' intrinsic growth rates, we explore a TEMP where performance depends directly on traits (Garnier et al. 2018, Laughlin et al. 2020). Thus we illustrate cases where the *r* parameter is assumed to vary with trait values (e.g. faster growth for smaller organisms; (Adler et al. 2014)). Alternatively, this parameter could also vary with the environment (Poorter and Markesteijn 2008, Wisnoski and Shoemaker 2022).

We find that variation in the biological process underlying the TEMP can lead to different parameter distributions in GLV models (Fig. 3). Under the hypothesis of competitive hierarchy, the distribution of interaction coefficients changes with environmental conditions, with potentially more negative interaction coefficients under lower environmental values (here corresponding to less stressful conditions). Within an environmental condition, the distribution of interaction coefficients is asymmetrical and highly skewed. Similar environmental effects occur for the limiting similarity model, but the interaction coefficient distribution is symmetric and less skewed. These simulations demonstrate that even in a simple dynamical model, environmental context and different hypotheses can yield different outcomes for the parameters, and in turn for prediction and control problems that we investigate below.

Part 2. Applications to prediction problems

Predicting abundance

After implementing a TEMP, the dynamical model is fully parameterized. This means it is possible to address any prediction task that requires a dynamical model. There is an extensive literature on the properties of parameterized dynamical models, especially the GLV model, which can now be leveraged (Ellner and Guckenheimer 2011). It is also possible to make predictions of abundance over time by applying the dynamical model (Fig. 4a). This can be useful for example if one is interested in the trajectory of the community either in the absence of environmental change or in the presence of it (e.g. stochastic environmental variation that prevents the community from reaching an attractor). However, if an

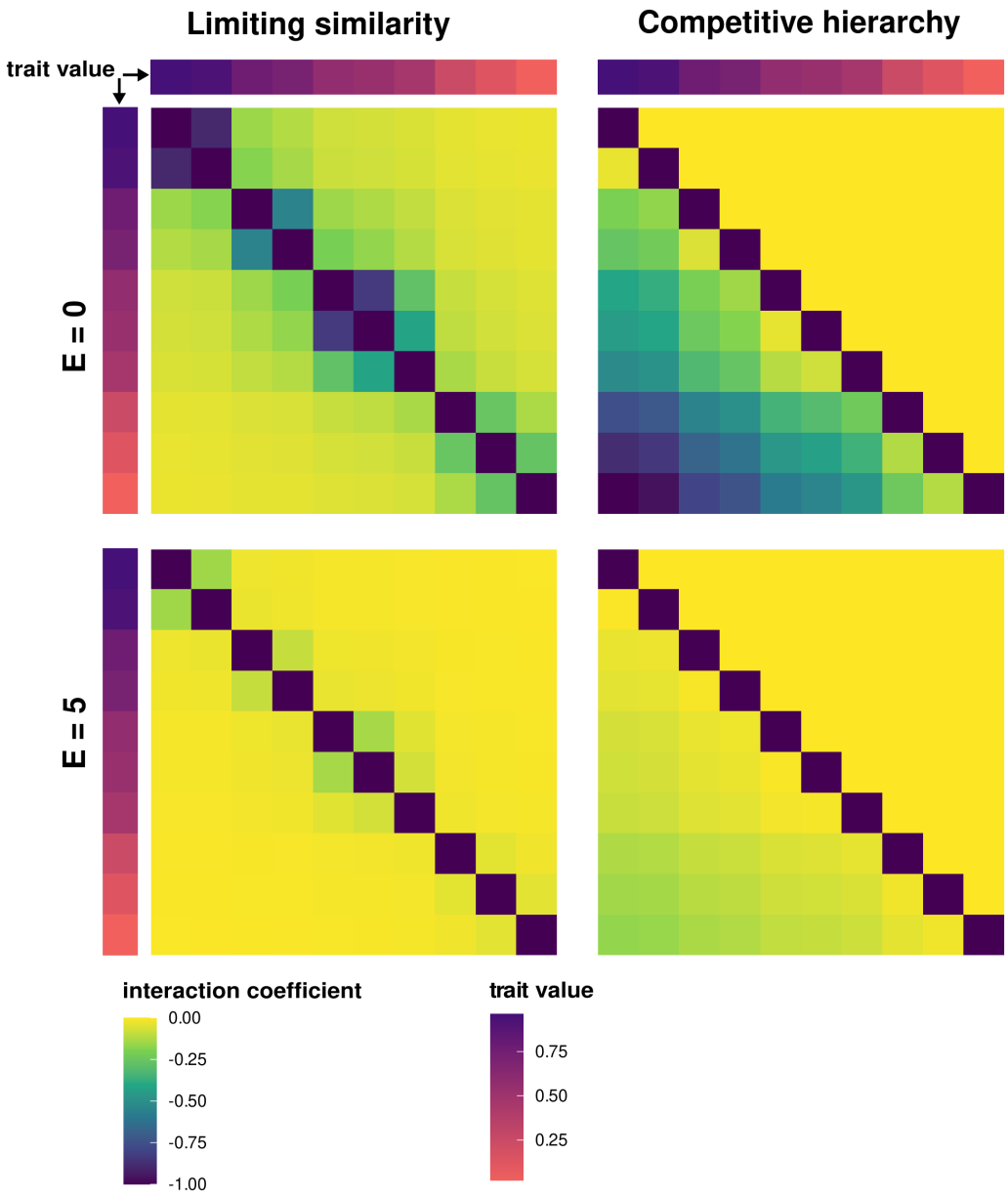

Figure 3. Predictions of interaction coefficients (the A parameters in the GLV model) under a limiting similarity TEMP (left) or a competitive hierarchy TEMP (right), for different environmental values. Trait values (shown in plot margins) for n = 10 species are sampled from a uniform distribution (mean = 0, standard deviation = 1) and environmental values vary from E = 0 (top), and E = 5 (bottom).

attractor is reached by the community, for example if the environment does not change over time, one can usefully predict features of the equilibrium.

Predicting coexistence properties

Integrating TEMP into a dynamical model can lead to different coexistence outcomes depending on the mechanisms structuring the community (e.g. limiting similarity versus competitive hierarchy). We illustrate this application by focusing on five key properties of the community at equilibrium: equilibrium abundance, which indicates which species will be common or rare or absent (Maynard et al. 2020); richness: the number of coexisting species; feasibility: whether all species have abundances greater than zero (Grilli et al. 2017); stability: whether all resident species tend to persist in the assemblage when perturbed to low abundance because the low-density growth rate of each species is positive, and abundances are resilient to small perturbations (May 1973, Grainger et al. 2019); and invasibility: whether non-resident species can become resident in the community, or equivalently, whether non-resident species have positive low density growth rates (Serván et al. 2018). These analyses can also be replicated to predict all possible subcommunities (i.e. those with certain combinations of species absent) to assess alternate assembly possibilities, but we do not explore this further here – see Blonder et al. 2022, Hofbauer and Schreiber 2022.

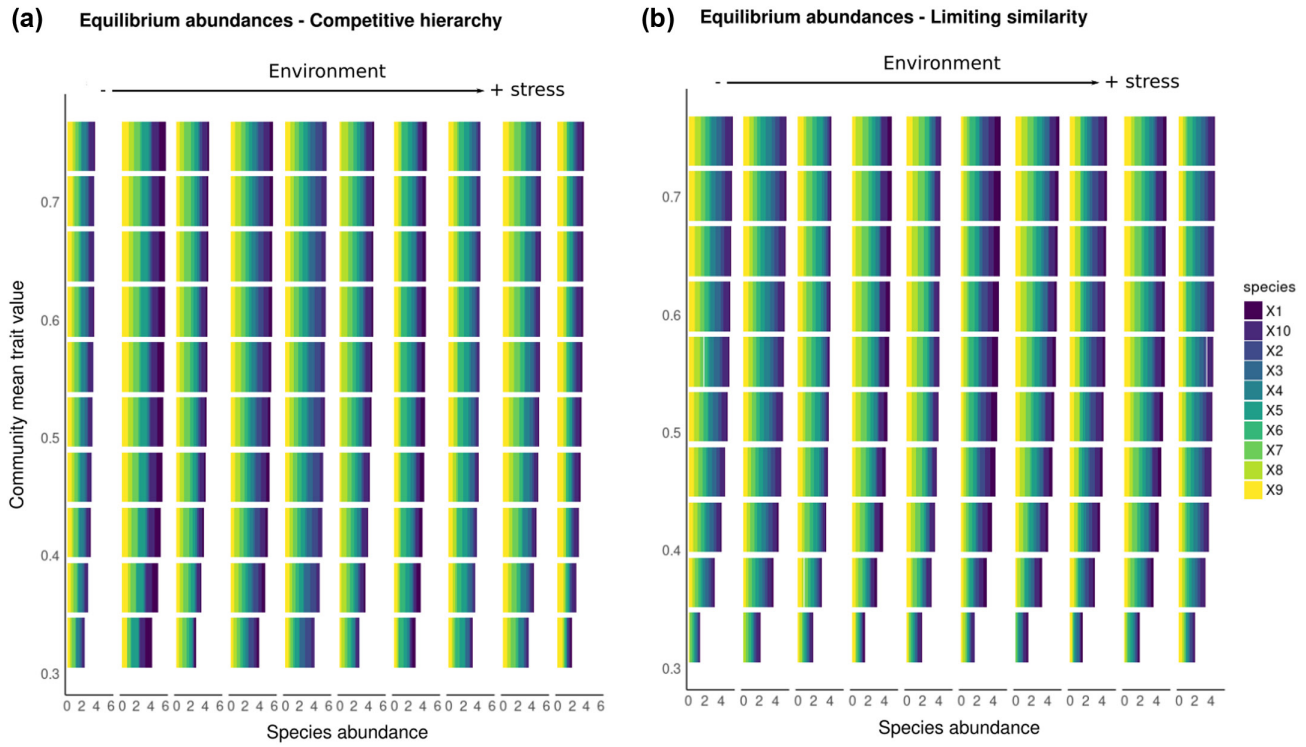

Figure 4. Predictions of equilibrium abundance under a competitive hierarchy TEMP (a) or a normalized limiting similarity TEMP (b), assuming GLV dynamics. Trait values are sampled from a uniform distribution [0,1] and an environmental gradient [0,10]. Intrinsic growth rates follow a linear TEMP ($r_i = T_i$). Initial abundances are randomly sampled from a univariate uniform distribution spanning [0,1]. Simulations are made for 100 replicate communities. x-axis values on inset panels indicate absolute abundances.

Using TEMP, coexistence properties can then be reframed in terms of trait and environment parameters. We find that qualitatively different coexistence outcomes can occur for the same values of trait or environment parameters if the TEMPs differ (Fig. 5). In a competitive hierarchy hypothesis TEMP, communities with higher mean trait values and under lower environment parameter values have a higher probability of feasibility (Fig. 5a) and lower realized richness (Fig. 5c) than those with low meant trait values under high environment parameter values. The probability of stability is higher for communities with higher mean trait values under higher environmental values (Fig. 5b). In a limiting similarity TEMP, communities with lower mean trait values and lower environment parameter values have a higher probability of feasibility (Fig. 5d) and lower realized richness (Fig. 5f), while the probability of stability is higher under low environment parameter values for all mean trait values (Fig. 5e). These results illustrate how coexistence outcomes can be predicted for different combinations of trait and environment parameters.

Predicting invasibility and succession (response to biotic context)

A community's susceptibility to invasion, and the identity of species that could enter or exit, can be predicted by constructing invasibility surfaces from dynamical models, based on trait, environment, and density axes. An invasibility surface can be numerically estimated using TEMP by simulating the low-density introduction of an invader species across a grid of trait, density, and/or environment values, then estimating the invader's equilibrium abundance. This surface thus identifies the contexts that would allow a species to invade at a given time point and is similar to a fitness landscape used in demographic predictions of evolutionary stable strategies (Hesse et al. 2008) but is explicitly trait-based (Laughlin and Messier 2015, Falster et al. 2017, Gaüzère et al. 2020b, Klausmeier et al. 2020). Any species with traits that confer a non-negative equilibrium abundance could invade that environment. The invasibility surface may change over time, either as biotic or abiotic context shifts. Plotting the invasibility surface for different community compositions enables prediction of each community's resistance to invasion.

We find that it is possible to predict the traits and environments that enable invasion in a dynamical model (Fig. 6). In a competitive hierarchy TEMP, we find that invaders with higher trait values under high environmental values (more stressful environmental conditions) have higher equilibrium abundances (Fig. 6a), which is consistent with the less complex interaction networks observed in these cases. In a limiting similarity TEMP, invaders with higher trait values and under high environmental values have higher equilibrium abundances (Fig. 6b), because the relative distribution of interaction coefficients skews towards weak interspecific interactions, which are compatible with coexistence. However, in low environment values, species with certain

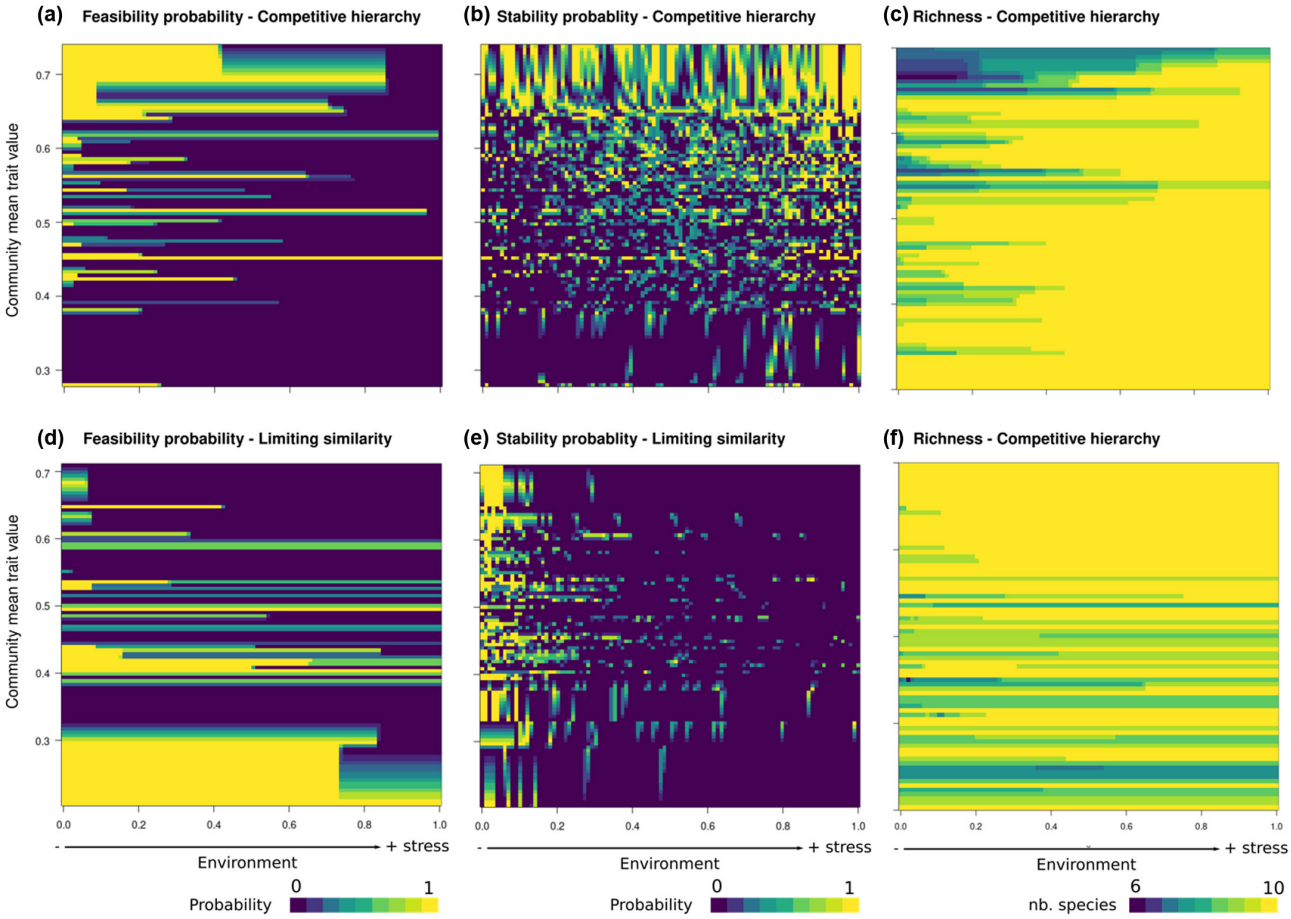

Figure 5. Coexistence outcome predictions for 10-species communities predicted under a competitive hierarchy TEMP (a, b, c) or a normalized limiting similarity TEMP (d, e, f), assuming GLV dynamics. Trait values are sampled from a uniform distribution [0,1] and an environmental gradient [0,1]. Intrinsic growth rates follow a linear TEMP ($r_i = T_i$). Initial abundances are randomly sampled from a univariate uniform distribution spanning [0,1]. Simulations are made for 100 replicate communities. (a, d) The probability of feasibility is inferred from communities with different community trait mean and environment values. (b, e) The probability of stability is inferred from communities with the corresponding community mean trait value and environment value. (c, f) The richness (averaged across replicates) is inferred from communities with the corresponding mean trait value and environment value.

traits can never invade the community because they are too similar to a resident species, while species with other trait values can exploit 'gaps' in the resident community. Thus, these invasibility surfaces allow explicit prediction of the traits of species that could successfully invade in each environment, or the species which would go locally extinct in each environment and can thus identify potential pathways of succession or invasion. Note that these invasion surfaces are thus dependent on the instantaneous biotic context (number and identity of resident species) and will change as species then invade or go locally extinct.

Predicting trait consequences of environmental change (response to abiotic context)

Predicting the response of communities to environmental change is useful for assessing how environmental changes will affect trait distributions, as well as for forecasting changes in ecosystem functioning (Blonder et al. 2017, Lavorel and Garnier 2002). Both goals are closely linked by the concept of trait-environment relationships, which describe correlations between trait values and environmental conditions based on their spatial distributions (Dray and Legendre 2008, Bruelheide et al. 2018). Trait–environment relationships emerge from dynamical models because the combinations of species (with different traits) that coexist may change along environmental gradients (Laughlin and Messier 2015).

We find relatively simple trait–environment relationships yielding strong predictability under both competitive hierarchy and limiting similarity TEMPs when environmental change was linear (Fig. 7a–b). However, when environmental change is periodic, trait-environment relationships showed alternate community trait states that reduced their predictability under both competitive hierarchy and limiting similarity TEMPs (Fig. 7c–d). In these cases, nonlinear trajectories of environmental change shift the interaction coefficient values over time, which in turn lead to community composition shifting. Because the periodic environmental change does not have a consistent direction, the community composition can

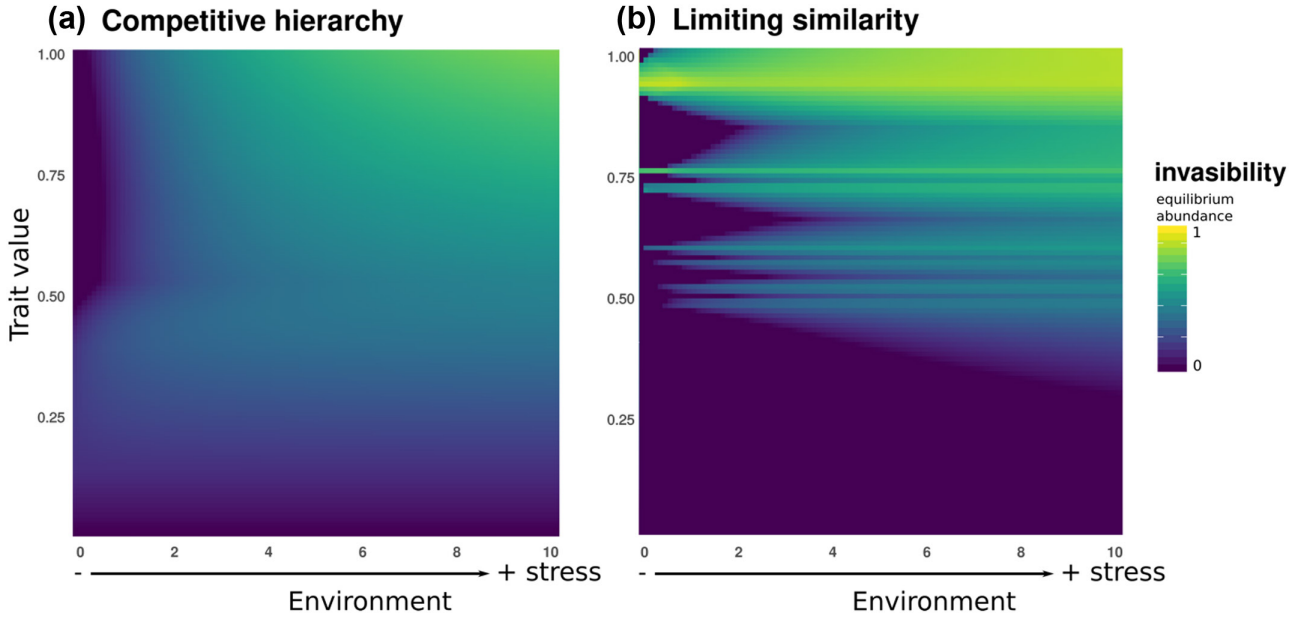

Figure 6. Invasibility surfaces predicted under the hypothesis of (a) a competitive hierarchy TEMP and (b) a normalized limiting similarity TEMP, both assuming GLV dynamics. Traits for n = 10 species are sampled from a univariate uniform distribution spanning [0,1] and environment gradient varying across the interval [0,10]. Intrinsic growth rates are set constant r = 0.5 for all species (to isolate the trait effects only on interaction coefficients). Initial abundances are set to 0.0005 and each simulation is allowed to come to equilibrium, after which a species with a different trait value (y-axis) is introduced in each environment, and its invasibility (equilibrium abundance) is estimated and then plotted. An invasibility near zero indicates an unsuccessful invasion.

end up lagging the equilibrium in complex ways. Thus, the observed trait–environment relationships depend strongly on the TEMP and the trajectory of environmental change.

Part 3. Applications to control problems

Improved prediction from dynamical models opens the possibility of ecological control by identifying action sequences of perturbations that would cause the community to reach a desired state. Such sequences could be optimal in the sense of requiring less time, money, or effort than all other possible perturbations (Fig. 1b). Optimal control theory has been used in numerous ecological problems. These challenges include shifting microbial community dynamics (Coyte et al. 2015, García-Jiménez et al. 2018, Angulo et al. 2019, Jones et al. 2020), managing forest fire risk (McCarthy et al. 2001, Malo et al. 2021), reducing insect outbreaks (Desharnais et al. 2001), sustainably managing fisheries (Chakraborty et al. 2011, Boettiger et al. 2015, Brias and Munch 2021), and stabilizing predator/prey models (Albrecht et al. 1976, Liu and Rohlf 1998, Crespo and Sun 2002, Jiang and Lu 2007).

Action sequences can be identified from two classes of control policies. The first class of control policies is 'impulsive', reflecting discrete actions taken instantaneously. The second class is 'continuous', reflecting actions taken smoothly over time. Impulsive control may be more realistic for situations where discrete perturbations can be made, such as quickly adding or removing water from an environment (Beier et al. 2012) or manipulating nutrient abundance (Treloar et al. 2020), while continuous control may be more realistic for situations where variable perturbations are possible, such as releasing variable numbers of individuals of a species over time (Shea and Possingham 2000), or controlling environmental conditions in a bioreactor (Angulo et al. 2019).

Theory-based control can augment the limited possibilities that can be explored by expert knowledge or experimentation. However, applying optimal control theory often requires knowledge of a fully parameterized dynamical model, e.g. model predictive control (Agachi et al. 2016), dynamic programming (Bertsekas 2000), or at least the ability to simulate time series from a hidden dynamical model, as in reinforcement learning (Recht 2019, Brias and Munch 2021). TEMP could improve the interpretability and usability of optimal control theory by identifying variables that can be perturbed (species abundances, environment). Many alternative candidate variables might be difficult to perturb independently (e.g. an interaction coefficient parameter). In contrast, it may be easier to perturb the environment or the abundance of a species with certain traits (e.g. an antibiotic that affects all bacteria using a certain metabolic pathway, or a trap that affects all animals of a certain size). Thus, trait and environment variables provide potentially useful starting points for identifying realistic control policies for community dynamics. In the below three examples, we show how to start in an arbitrary non-equilibrium state and then identify perturbations that reach a desired equilibrium state.

Applications to control problems

We find that the environment can be perturbed to cause the removal of an unwanted species (Fig. 8). This is analogous to a

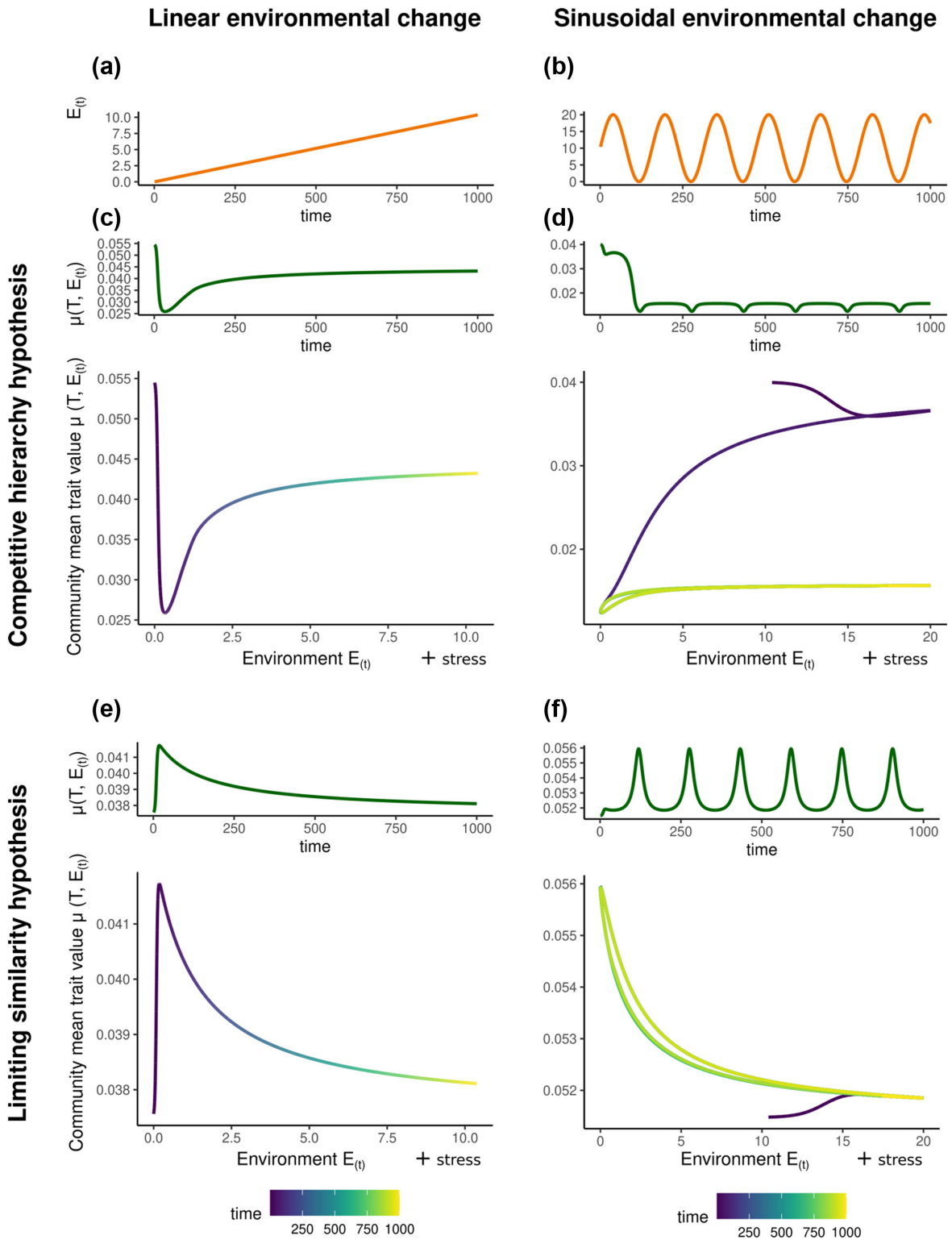

Figure 7. Predictions of trait–environment relationships under a competitive hierarchy TEMP (a, b) or a normalized limiting similarity TEMP (c, d), for either linear (a, c) or periodic (b, d) environmental change, assuming GLV dynamics. The upper panel shows the temporal change in environment in orange; the middle panel shows the temporal change in abundance-weighted mean trait values of the community in green; the lower panel shows the temporal trait–environment relationships (for each time point, the abundance-weighted mean trait values are plotted against the corresponding environmental value). Color indicates the time (from 0, dark blue to 300, yellow). Predictions are obtained for n = 10 species with traits sampled from a univariate uniform distribution spanning [0,1], and environments that change over time as shown. Intrinsic growth rates are set constant $r = 0.5$ for all species. Initial abundances are set to N = 0.0005.

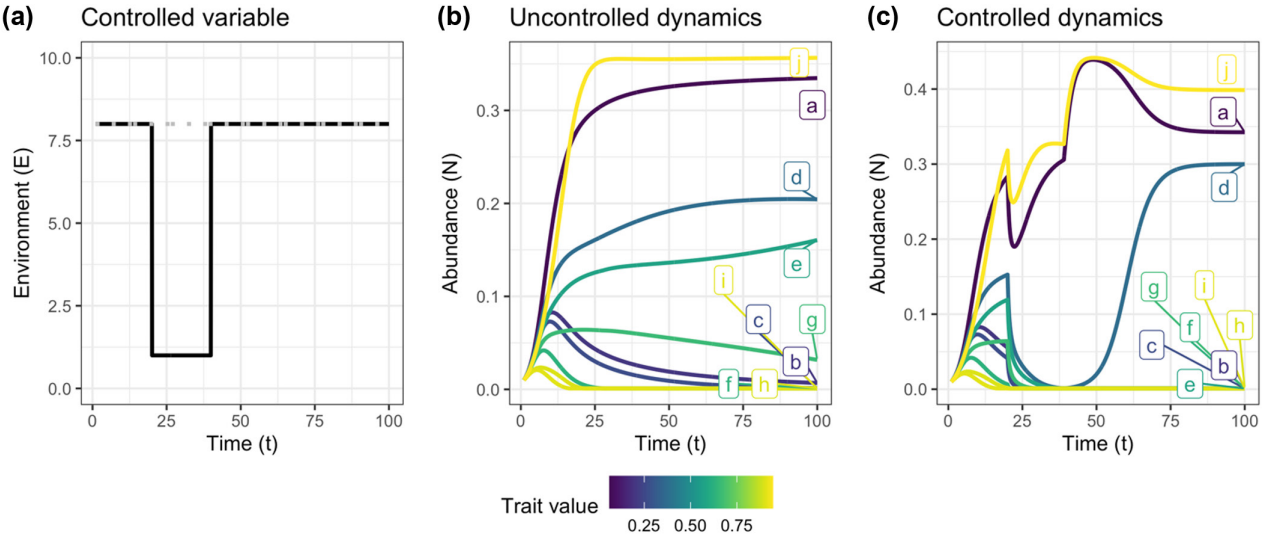

Figure 8. Impulsive control to prevent an unwanted species (E) from coexisting in the community by perturbing the environment, assuming GLV dynamics. Traits for n = 10 species are sampled from a univariate uniform distribution spanning [0,1]. Intrinsic growth rates are set constant to r = 0.5 for all species. A limiting similarity TEMP without normalization is used to predict interaction coefficients. (a) The environment is either constant at a value of E = 8 (gray dashed line) or is perturbed to E = 1 (black line) from times t = 20 to t = 40. (b) In the unperturbed case, species d and e coexist with dominant species a and j. (c) In the perturbed case, the change in environment shifts the interaction coefficients via the TEMP, leading to negative growth rates for species d and e. Eventually e is excluded but d persists at low density. After the perturbation, d recovers and stably coexists with a and j.

situation where a microbial community can be controlled by changing the temperature of the growth conditions. A TEMP for the interaction coefficients in a GLV model enables discovery of a control policy based on shifting the environment over time. By choosing appropriate times to shift the environment, the interaction coefficients are also shifted transiently, which enables a target species to be driven to extinction by these interactions with no further intervention (Supporting information). After this perturbation, the original environmental conditions can be restored, and a desired stable state can be maintained. However, this control strategy does have the tradeoff of causing the extinction of a small number of resident species. Additionally, it is possible in this scenario that the unwanted species could re-colonize from a metacommunity. In such a scenario, guaranteeing non-invasibility might require more sophisticated approaches.

We also find that TEMP can identify species with certain traits, which can be added or removed at specific times to shift the equilibrium abundances of other desired species, and/or cause the removal of undesired species (Fig. 9). This case is analogous to a situation where a microbial community can be controlled by selective inoculations (e.g. probiotics) or drug application (e.g. antibiotics), or a plant community can be controlled by selective introductions or weeding or herbicide application. In this example, it is possible to use a TEMP to produce an invasibility surface to determine the combinations of trait values of a test species that would successfully be able to invade a community and displace an undesired species, while also increasing the abundance of other desired species. In this example based on a limiting similarity TEMP, we select a test species to have a trait value slightly more extreme than that of the unwanted species, which enables it to exclude only the unwanted species. After the test species is introduced at low density and some time passes, the desired stable state is obtained (Supporting information). While some resident species are lost, no more are lost (though with different identities) than in the uncontrolled dynamics.

We lastly find TEMP can identify species with certain traits, whose abundance can then be continuously perturbed to achieve a desired community trait composition and species richness target (Fig. 10). This case is loosely analogous to a forest management problem where overall forest composition can be manipulated through selective removal (reduce abundance) or planting (increase abundance) of species with certain traits. We use a model predictive control algorithm to seek a community whose trait composition and species richness come close to the desired values, under a scenario where it is possible to perturb the abundance of two focal species over time whose traits are dissimilar from the target value (note that if one could control the abundance of species whose traits were similar to the target value, the problem would be trivial). By leveraging a TEMP, we can find an abundance-based control policy that comes close to the desired trait and richness targets. We then determine the success rate of model predictive control in perturbing a community from any of its stable and feasible fixed points to any other such fixed point, given the target state of maximal richness and an arbitrary trait composition. Under the limiting similarity TEMP, control is successful in approximately 50–75% of cases regardless of the the trait target or the initial richness, when starting from random initial abundances (Supporting information). This is because most combinations of species

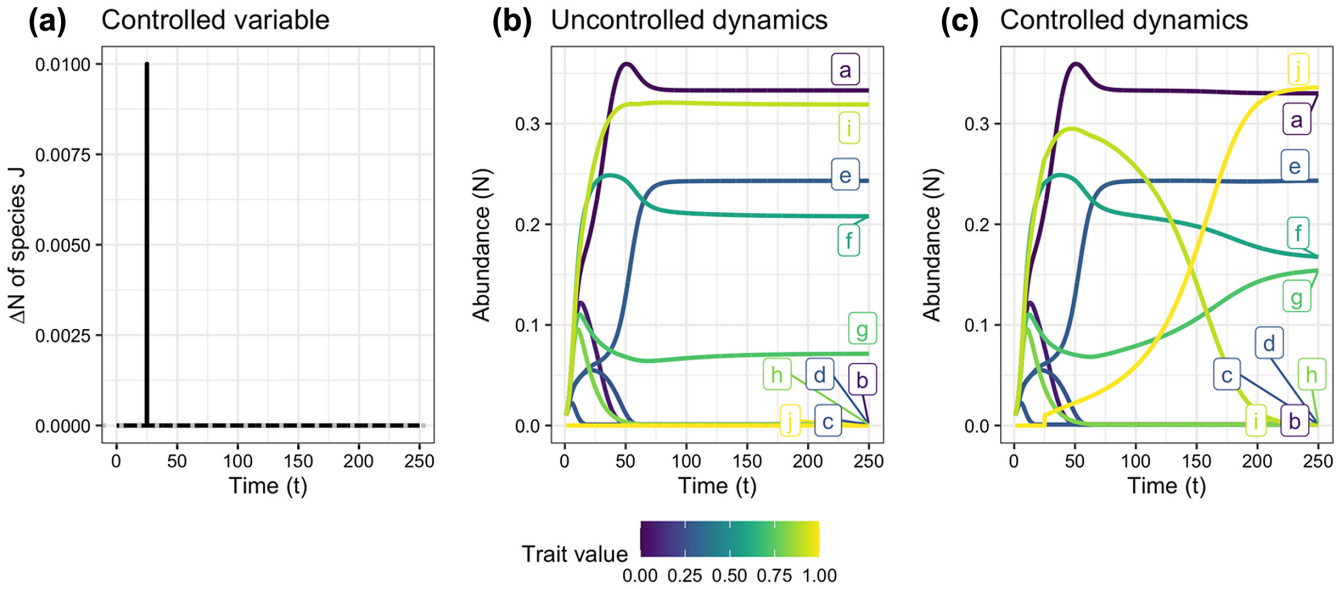

Figure 9. Impulsive control to remove unwanted species and shift species abundances via the introduction of species with certain traits, assuming GLV dynamics. Traits for n = 10 species are sampled from a univariate uniform distribution spanning [0,1]. Intrinsic growth rates are set constant to $r = 0.5$ for all species and the environment is set to E = 9. Species interactions are assumed to follow the limiting similarity hypothesis TEMP. (a) In the unperturbed case, n = 9 of the total n = 10 species are introduced (all except j, which is absent from the community); in the perturbed case, j is introduced at low density at t = 25. j is selected to have a trait similar to i, enabling it to have a large effect on the community. (b) The unperturbed dynamics lead to the presence of unwanted species i. (c) The perturbed dynamics after the introduction of j result in species i becoming extinct. A beneficial side effect is that the abundance of g is also increased.

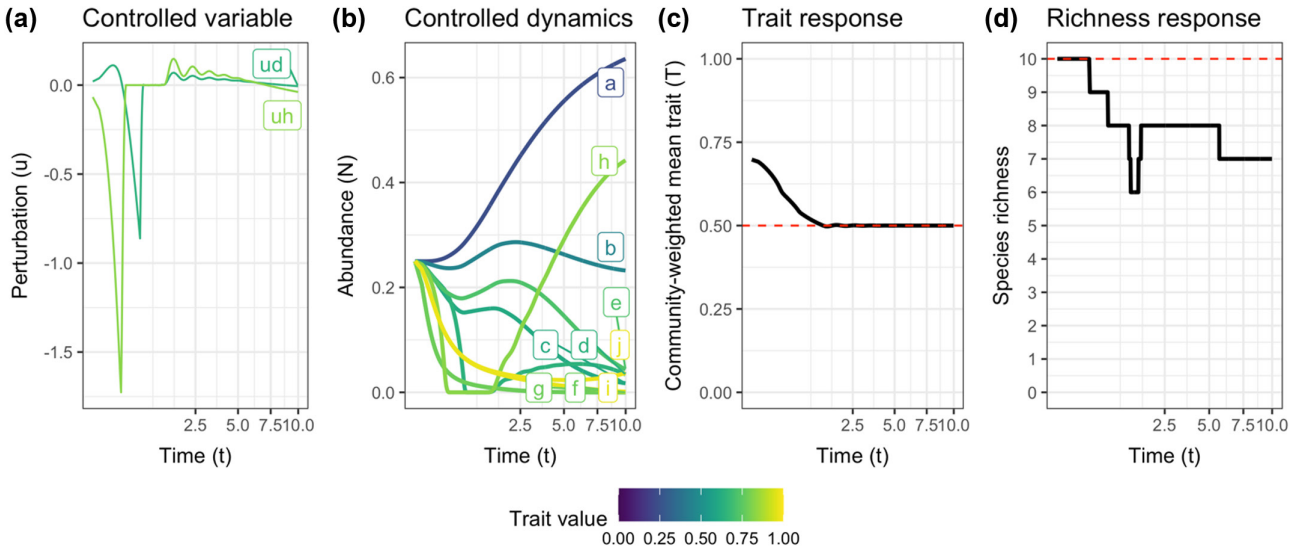

Figure 10. Continuous optimal control to achieve a certain community-weighted mean trait value as a desired state via perturbing the abundances of species with certain traits, assuming GLV dynamics. Traits (T) for n = 10 species are sampled from a univariate uniform distribution spanning [0,1]. Intrinsic growth rates are set constant to $r = 1$ for all species and the environment is set to E = 5. Species interactions are assumed to follow a limiting similarity TEMP. We assume that the desired state is a community-weighted mean trait value of $T = 0.5$ with maximal richness, and that the abundances of two species with intermediate trait values (d and h) can be controlled. (a) A model predictive control algorithm identifies continuous abundance perturbations, u_d and u_h, which achieve the desired outcome. (b) The controlled dynamics lead to transient changes in the abundance of the controlled species and the extinction of numerous other resident species. The best solution, which involves near-zero long-term perturbations, yields (c) a community weighted mean trait (black) that converges on the target (red) and (d) a species richness of seven, near the target (red). Note that the x-axis is square-root transformed to highlight early transient dynamics. For algorithm details, see the Supporting information.

can coexist. In contrast, under the competitive hierarchy TEMP, control is successful in approximately 75% of cases at low initial richness and only 10% at high initial richness, because most sub-dominant species are excluded, and trait targets cannot be reached. Thus, viable control policies can be found at least in the scenario outlined here, though further work would be needed to identify conditions under which this result generalizes.

Moving from concepts to applications

The above examples highlight the types of prediction and control problems that could eventually be addressed through integrating TEMP into dynamical models. They are meant to be illustrative of the key ideas, and as such are not meant to be representative of immediate real-world applications.

Applications to restoration

Ecological restoration is a key use case in that these problems often involve selection of species with certain traits and desired states with certain trait compositions, as well as scenarios of environmental change. While various trait-based restoration frameworks recently have emerged, TEMP provides different insights. It differs from Laughlin (2014a), Giannini et al. (2017), Laughlin et al. (2018) and Funk (2021) in focusing on the trajectories and underlying dynamical models, rather than only on the coexistence outcomes obtained, or on phenomenological descriptions of the assembly processes (e.g. biotic filters). It also differs from Maynard et al. (2020), Clark et al. (2021) and Blonder and Godoy (2022) because it relies on ecological hypotheses rather than mechanism-free machine learning. Last, it differs from Aoyama et al. (2022) in having an explicit focus on traits within dynamical models. As such, there may be opportunities for TEMP to complement these frameworks.

Statistical issues

To apply the TEMP approach to real data, a range of statistical issues will need to be solved, which are all widely acknowledged (Lawton 1999, Simberloff 2004, Vellend and Agrawal 2010, Mouquet et al. 2015, Shoemaker et al. 2020). These issues include identifying the appropriate type of TEMP to be used within the dynamical model of interest, which in turn requires identifying how many and which trait and environment parameter(s) are relevant, and also statistically estimating values for each such parameter. For simulation-based models that are already written in terms of trait and environment parameters (Falster et al. 2021), these issues are largely resolved, and control analyses like those we showed above are immediately tractable. For parameter-rich dynamical models that do not yet have obvious linkages to traits (e.g. the GLV model) there is a greater value for using TEMP. A few of the statistical estimation issues have been considered in the general context of predicting trait variation along environmental gradients (Webb et al. 2010), assessing the dimensionality of trait spaces (Laughlin 2014b, Mouillot et al. 2021), exploring interactions between traits and the environment (Pistón et al. 2019, Worthy et al. 2020, Li et al. 2021), and in fitting trait-informed plant community models (Clark et al. 2017, Chalmandrier et al. 2022, 2021).

Stochastic community dynamics can limit the utility of TEMP because they would reduce predictability and thus also controllability (Petchey et al. 2015, Pennekamp et al. 2019, Shoemaker et al. 2020). Stochasticity is thought to be common in many communities (Hubbell 2001, Zhou and Ning 2017, Shoemaker et al. 2020). For prediction problems, uncertainty in the dynamics or the TEMP could be numerically propagated to uncertainty in community-level responses, which would provide estimates of the limits to predictability. Such work could identify which community-level properties are the most realistic targets for prediction. For example, uncertainty in TEMP influencing interaction coefficients could be a key limit to skillful prediction of invasibility surfaces. For control problems, identifying optimal policies is becoming possible when there is either stochasticity in the underlying dynamics or noisy observations of the dynamics (e.g. for partially observable Markov decision processes, Katt et al. 2017, García-Jiménez et al. 2018).

Low predictability of external drivers like the environment may also constrain the predictability and controllability of community dynamics. For example, annual rainfall amounts may alter the likelihood of coexistence among desert annual plants (Warner and Chesson 1985, Gremer et al. 2013) but rainfall may itself be highly unpredictable. This may in turn then also limit controllability, if the reachable states are more sensitive to this environmental variation than to any other perturbation.

Tradeoffs

Using TEMP will not always be an improvement over standard dynamical model approaches. For instance, if many traits are needed to describe species (Falster et al. 2021), or if the dynamical model has enough parameters that each require different traits, then the fractional reduction in parameters (Fig. 2) could be very small, or even negative. Additionally, using TEMP is always an approximation of a high-dimensional system with a low-dimensional representation. Approximation is almost certainly lossy, meaning that TEMP-based prediction and control will be less skillful than the alternative. However, the improvements in interpretability and ease of measurement we have described for TEMP may justify their use in many cases.

Ethical issues

There are substantial moral and ethical implications to proposing control policies, e.g. in malaria eradication (Pugh 2016, Scoville et al. 2021). We must ask: who implements them, for whom are they implemented, who becomes impacted, and how likely are they to succeed safely without causing unexpected negative consequences (Adams and Mulligan 2003, Borrini et al. 2004, Díaz et al. 2015)? The very language of 'optimal' control assumes that everyone can agree on a desired outcome, which may be unrealistic. Beneficial progress towards ecological control will only come

if accompanied by full consideration and collaborative resolution of these moral questions.

We also are not proposing that all ecological communities should be predicted or controlled. We and others feel a moral discomfort with the prospect of subjugating nature in this way, as it may cause unexpected and undesirable consequences (Crichton 1991, Simberloff and Stiling 1996). However, in the Anthropocene, humans are constantly inflicting large perturbations to natural systems, albeit often without full acknowledgment of their consequences (Corlett 2015). Furthermore, restoration ecology and re-establishment of nature in human-influenced landscapes is becoming increasingly important in global change priorities (e.g. the United Nations Decade on Ecosystem Restoration). Consequently, there is a growing need for predicting community change and the ability to control such changes towards a specific target. Becoming more precise about the consequences of both intentional and unintentional perturbations – and consciously, rather than unconsciously, choosing control policies – will be critical to our future. Accepting the burden of control does not force us to unquestioningly accept ecomodernist ideas (Marris 2013) and pro-technology, pro-capital policies that may not serve the vast majority of people and nature (Monbiot 2015). Rather, discovering the boundaries of predictability and controllability with TEMP will help to generate a healthier respect and humility for the natural world, and a renewed focus on building socio-ecological systems that embrace uncertainty.

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Author contributions

Benjamin Wong Blonder and **Pierre Gaüzère** contributed equally to this publication. **Benjamin Wong Blonder:** Conceptualization (equal), Visualization (equal), Writing – original draft (equal). **Pierre Gaüzère:** Conceptualization (equal), Visualization (equal), Writing – original draft (equal), Writing – review and editing (equal). **Lars L. Iversen:** Writing – review and editing-Supporting. **Po-Ju Ke:** Writing – review and editing-Supporting. **Will K. Petry:** Writing – review and editing-Supporting. **Courtenay A. Ray:** Writing – review and editing-Supporting. **Roberto Salguero-Gómez:** Writing – review and editing-Supporting. **William Sharpless:** Software-Supporting, Writing – review and editing-Supporting. **Cyrille Violle:** Writing – review and editing-Supporting

Data availability statement

Data are available from the Zenodo Digital Repository: https://zenodo.org/record/7576397 (Gaüzère 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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