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

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Title

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Abstract

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.

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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 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 actions 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 (for example, a matrix of interaction coefficients). The parameter space dimensionality problem can make it difficult to parameterize a model (e.g. (Godoy & 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 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 the further consequences for prediction and control problems.

There is a long history of using trait and environmental variables in community ecology (Gaudet & Keddy 1988; Keddy 1990; Lavorel & Garnier 2002; Violle *et al.* 2007). Examples include measuring community-level properties like trait dispersion patterns (Kraft & Ackerly 2010; Mayfield & 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 & 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 TEMPs (**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 TEMPs.

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 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 & Levine 2014; Weiss-Lehman *et al.* 2022a). 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 & 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 & Keddy 1988; Grime 2006; Violle *et al.* 2009; Mayfield & Levine 2010; Kunstler *et al.* 2012). Interaction coefficients also have been hypothesized to be environmentally dependent (Grime 1977; Goldberg & 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.* 2022b); a version of the ‘stress gradient hypothesis’).

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 & Markesteijn 2008; Wisnoski & 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 & Guckenheimer 2011; McCann & Gellner 2020). 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 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 TEMPs in dynamical models can lead to different coexistence outcomes depending on the mechanisms structuring the community (*e.g.*, limiting similarity *vs.* 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 & Schreiber 2022) .

Using TEMPs, 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 mean 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 TEMPs 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 & Messier 2015; Falster *et al.* 2017; Gauzere *et al.* 2020; 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 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 (Lavorel & Garnier 2002; Blonder *et al.* 2017). 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 & Legendre 2008; Bruehlheide *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 & Messier 2015).

We find relatively simple trait-environment relationships yielding strong predictability under both competitive hierarchy and limiting similarity TEMP when environmental change was linear (**Fig. 7a, 7b**). 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 TEMP (**Fig. 7c, 7d**). 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 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 & Munch

2021), and stabilizing predator/prey models (Albrecht *et al.* 1976; Liu & Rohlf 1998; Crespo & Sun 2002; Jiang & 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 & 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 & Munch 2021). TEMPAs 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 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 (see **Text S1**). 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 TEMPs 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 (see **Text S1**). While some resident species are lost, no more are lost (though with different identities) than in the uncontrolled dynamics.

We lastly find TEMPs 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 (**Fig. S1**). This is because most combinations of species 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's 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, the TEMP approach provides different insights. It differs from (Laughlin 2014a; Giannini *et al.* 2017; Laughlin *et al.* 2018; 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; Blonder & 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 & 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, e.g. (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 TEMPs. 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.* 2021, 2022).

Stochastic community dynamics can limit the utility of TEMPs 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 & 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 TEMPs 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 & 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 TEMPs 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 a 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 TEMPs 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 & Mulligan 2003; Borriani *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 & 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 TEMPs 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.

441 **Literature Cited**

- 442 Abrams, P. (1975). Limiting similarity and the form of the competition coefficient. *Theoretical Population*
 443 *Biology*, 8, 356–375.
- 444 Adams, W.M. & Mulligan, M. (2003). *Decolonizing nature: strategies for conservation in a post-colonial*
 445 *era*. Earthscan.
- 446 Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C., *et al.*
 447 (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the*
 448 *National Academy of Sciences*, 111, 740–745.
- 449 Agachi, P.S., Cristea, M.V., Csavdari, A.A. & Szilagyi, B. (2016). Model predictive control. In: *Advanced*
 450 *Process Engineering Control*. De Gruyter.
- 451 Albrecht, F., Gatzke, H., Haddad, A. & Wax, N. (1976). On the control of certain interacting populations.
 452 *Journal of Mathematical Analysis and Applications*, 53, 578–603.
- 453 Andersson, J.A., Gillis, J., Horn, G., Rawlings, J.B. & Diehl, M. (2019). CasADi: a software framework
 454 for nonlinear optimization and optimal control. *Mathematical Programming Computation*, 11, 1–
 455 36.
- 456 Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species
 457 coexistence via the storage effect. *Proceedings of the National Academy of Sciences*, 106, 11641.
- 458 Angulo, M.T., Kelley, A., Montejano, L., Song, C. & Saavedra, S. (2021). Coexistence holes characterize
 459 the assembly and disassembly of multispecies systems. *Nature Ecology & Evolution*, 1–11.
- 460 Angulo, M.T., Moog, C.H. & Liu, Y.-Y. (2019). A theoretical framework for controlling complex microbial
 461 communities. *Nature Communications*, 10, 1–12.
- 462 Aoyama, L., Shoemaker, L.G., Gilbert, B., Collinge, S.K., Faist, A.M., Shackelford, N., *et al.* (2022).
 463 Application of modern coexistence theory to rare plant restoration provides early indication of
 464 restoration trajectories. *Ecological Applications*, n/a, e2649.
- 465 Barabás, G., J. Michalska-Smith, M. & Allesina, S. (2016). The effect of intra-and interspecific competition
 466 on coexistence in multispecies communities. *The American Naturalist*, 188, E1–E12.
- 467 Baranwal, M., Clark, R.L., Thompson, J., Sun, Z., Hero, A.O. & Venturelli, O.S. (2022). Recurrent neural
 468 networks enable design of multifunctional synthetic human gut microbiome dynamics. *Elife*, 11,
 469 e73870.
- 470 Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Körner, C., *et al.* (2012).
 471 Precipitation manipulation experiments—challenges and recommendations for the future. *Ecology*
 472 *Letters*, 15, 899–911.
- 473 Bertsekas, D.P. (2000). *Dynamic programming and optimal control*. Athena Scientific, Belmont, MA.
- 474 Beverton, R. (1957). On the dynamics of exploited fish populations. *Fishery Invest. UK Ser., II*, 19, 1–533.
- 475 Biegler, L.T. (2010). *Nonlinear programming: concepts, algorithms, and applications to chemical*
 476 *processes*. SIAM, Philadelphia, PA.
- 477 Bimler, M.D., Stouffer, D.B., Lai, H.R. & Mayfield, M.M. (2018). Accurate predictions of coexistence in
 478 natural systems require the inclusion of facilitative interactions and environmental dependency.
 479 *Journal of Ecology*, 106, 1839–1852.
- 480 Blonder, B., Moulton, D.E., Blois, J., Enquist, B.J., Graae, B.J., Macias-Fauria, M., *et al.* (2017).
 481 Predictability in community dynamics. *Ecology Letters*, 20, 293–306.
- 482 Blonder, B.W. & Godoy, O. (2022). Predicting and prioritizing species coexistence: learning outcomes via
 483 experiments. *bioRxiv*.
- 484 Blonder, B.W., Lim, M.H., Sunberg, Z. & Tomlin, C. (2022). Navigation between states in ecological
 485 communities by taking shortcuts, with application to control. *arXiv preprint arXiv:2204.07629*.
- 486 van Bodegom, P.M., Douma, J.C. & Verheijen, L.M. (2014). A fully traits-based approach to modeling
 487 global vegetation distribution. *Proceedings of the National Academy of Sciences*, 111, 13733–
 488 13738.

- Boettiger, C., Mangel, M. & Munch, S. (2015). Avoiding tipping points in fisheries management through Gaussian process dynamic programming. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20141631.
- Borrini, G., Kothari, A. & Oviedo, G. (2004). *Indigenous and local communities and protected areas: Towards equity and enhanced conservation: Guidance on policy and practice for co-managed protected areas and community conserved areas*. IUCN.
- Brias, A. & Munch, S.B. (2021). Ecosystem based multi-species management using Empirical Dynamic Programming. *Ecological Modelling*, 441, 109423.
- Bruehlheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S.M., *et al.* (2018). Global trait–environment relationships of plant communities. *Nature Ecology & Evolution*, 2, 1906–1917.
- Buffie, C.G., Jarchum, I., Equinda, M., Lipuma, L., Gobourne, A., Viale, A., *et al.* (2012). Profound alterations of intestinal microbiota following a single dose of clindamycin results in sustained susceptibility to *Clostridium difficile*-induced colitis. *Infection and immunity*, 80, 62–73.
- Chakraborty, K., Das, S. & Kar, T.K. (2011). Optimal control of effort of a stage structured prey–predator fishery model with harvesting. *Nonlinear Analysis: Real World Applications*, 12, 3452–3467.
- Chalmandrier, L., Hartig, F., Laughlin, D.C., Lischke, H., Pichler, M., Stouffer, D.B., *et al.* (2021). Linking functional traits and demography to model species-rich communities. *Nature Communications*, 12, 1–9.
- Chalmandrier, L., Stouffer, D.B., Purcell, A.S.T., Lee, W.G., Tanentzap, A.J. & Laughlin, D.C. (2022). Predictions of biodiversity are improved by integrating trait-based competition with abiotic filtering. *Ecology Letters*, n/a.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, 31, 343–366.
- Clark, J.S., Nemergut, D., Seyednasrollah, B., Turner, P.J. & Zhang, S. (2017). Generalized joint attribute modeling for biodiversity analysis: Median-zero, multivariate, multifarious data. *Ecological Monographs*, 87, 34–56.
- Clark, R.L., Connors, B.M., Stevenson, D.M., Hromada, S.E., Hamilton, J.J., Amador-Noguez, D., *et al.* (2021). Design of synthetic human gut microbiome assembly and butyrate production. *Nature communications*, 12, 1–16.
- Corlett, R.T. (2015). The Anthropocene concept in ecology and conservation. *Trends in ecology & evolution*, 30, 36–41.
- Coyte, K.Z., Schluter, J. & Foster, K.R. (2015). The ecology of the microbiome: networks, competition, and stability. *Science*, 350, 663–666.
- Crespo, L.G. & Sun, J.Q. (2002). Optimal control of populations of competing species. *Nonlinear Dynamics*, 27, 197–210.
- Crichton, M. (1991). *Jurassic Park*. Random House.
- Desharnais, R.A., Costantino, R.F., Cushing, J.M., Henson, S.M. & Dennis, B. (2001). Chaos and population control of insect outbreaks. *Ecology Letters*, 4, 229–235.
- Díaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N., *et al.* (2015). The IPBES Conceptual Framework—connecting nature and people. *Current Opinion in Environmental Sustainability*, 14, 1–16.
- Dray, S. & Legendre, P. (2008). Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology*, 89, 3400–3412.
- Dukovski, I., Bajić, D., Chacón, J.M., Quintin, M., Vila, J.C., Sulheim, S., *et al.* (2021). A metabolic modeling platform for the computation of microbial ecosystems in time and space (COMETS). *Nature Protocols*, 1–58.
- Ellner, S.P. & Guckenheimer, J. (2011). *Dynamic models in biology*. Princeton University Press.
- Falster, D.S., Brännström, Å., Westoby, M. & Dieckmann, U. (2017). Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences*, 114, E2719–E2728.

- Falster, D.S., Kunstler, G., FitzJohn, R.G. & Westoby, M. (2021). Emergent shapes of trait-based competition functions from resource-based models: A Gaussian is not normal in plant communities. *The American Naturalist*, 198, 000–000.
- Ferguson, H.M., Dornhaus, A., Beeche, A., Borgemeister, C., Gottlieb, M., Mulla, M.S., *et al.* (2010). Ecology: a prerequisite for malaria elimination and eradication. *PLoS Medicine*, 7, e1000303.
- Funk, J.L. (2021). Revising the trait-based filtering framework to include interacting filters: Lessons from grassland restoration. *Journal of Ecology*, 109, 3466–3472.
- García-Jiménez, B., de la Rosa, T. & Wilkinson, M.D. (2018). MDPbiome: microbiome engineering through prescriptive perturbations. *Bioinformatics*, 34, i838–i847.
- Garnier, E., Fayolle, A., Navas, M.-L., Damgaard, C., Cruz, P., Hubert, D., *et al.* (2018). Plant demographic and functional responses to management intensification: A long-term study in a Mediterranean rangeland. *Journal of Ecology*, 106, 1363–1376.
- Gaudet, C.L. & Keddy, P.A. (1988). A comparative approach to predicting competitive ability from plant traits. *Nature*, 334, 242–243.
- Gaüzère, P., Iversen, L.L., Seddon, A.W., Violle, C. & Blonder, B. (2020). Equilibrium in plant functional trait responses to warming is stronger under higher climate variability during the Holocene. *Global Ecology and Biogeography*, 29, 2052–2066.
- Gauzere, P., Morin, X., Violle, C., Caspeta, I., Ray, C. & Blonder, B. (2020). Vacant yet invisable niches in forest community assembly. *Functional Ecology*, 34, 1945–1955.
- Giannini, T.C., Giuletto, A.M., Harley, R.M., Viana, P.L., Jaffe, R., Alves, R., *et al.* (2017). Selecting plant species for practical restoration of degraded lands using a multiple-trait approach. *Austral Ecology*, 42, 510–521.
- Godoy, O. & Levine, J.M. (2014). Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology*, 95, 726–736.
- Goldberg, D.E. & Barton, A.M. (1992). Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *The American Naturalist*, 139, 771–801.
- Grainger, T.N., Levine, J.M. & Gilbert, B. (2019). The invasion criterion: A common currency for ecological research. *Trends in Ecology & Evolution*, 34, 925–935.
- Gremer, J.R., Kimball, S., Keck, K.R., Huxman, T.E., Angert, A.L. & Venable, D.L. (2013). Water-use efficiency and relative growth rate mediate competitive interactions in Sonoran Desert winter annual plants. *American Journal of Botany*, 100, 2009–2015.
- Grilli, J., Adorisio, M., Suweis, S., Barabás, G., Banavar, J.R., Allesina, S., *et al.* (2017). Feasibility and coexistence of large ecological communities. *Nature Communications*, 8, 1–8.
- Grime, J. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 1169–1194.
- Grime, J.P. (2006). Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science*, 17, 255–260.
- Hesse, E., Rees, M., Müller-Schärer, H., Associate Editor: Catherine A. Pfister, & Editor: Monica A. Geber. (2008). Life-History Variation in Contrasting Habitats: Flowering Decisions in a Clonal Perennial Herb (*Veratrum album*). *The American Naturalist*, 172, E196–E213.
- HilleRisLambers, J., Adler, P., Harpole, W., Levine, J. & Mayfield, M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43.
- Hofbauer, J. & Schreiber, S.J. (2022). Permanence via invasion graphs: Incorporating community assembly into Modern Coexistence Theory. *arXiv preprint arXiv:2204.03773*.
- Hubbell, S.P. (2001). *The unified neutral theory of biodiversity and biogeography (MPB-32)*. Princeton University Press.
- Jiang, G. & Lu, Q. (2007). Impulsive state feedback control of a predator–prey model. *Journal of Computational and Applied Mathematics*, 200, 193–207.
- Johnson, P.T., De Roode, J.C. & Fenton, A. (2015). Why infectious disease research needs community ecology. *Science*, 349, 1259504.

- Jones, E.W., Shankin-Clarke, P. & Carlson, J.M. (2020). Navigation and control of outcomes in a generalized Lotka-Volterra model of the microbiome. In: *Advances in Nonlinear Biological Systems: Modeling and Optimal Control*. American Institute of Mathematical Sciences.
- Katt, S., Oliehoek, F.A. & Amato, C. (2017). Learning in POMDPs with Monte Carlo tree search. *Proceedings of the 34th International Conference on Machine Learning*, pp. 1819–1827.
- Keddy, P.A. (1990). Competitive hierarchies and centrifugal organization in plant communities. *Perspectives on plant competition*, 265, 90.
- Klausmeier, C.A., Kremer, C.T. & Koffel, T. (2020). Trait-based ecological and eco-evolutionary theory. In: *Theoretical Ecology*. Oxford University Press, pp. 161–194.
- Kraft, N.J. & Ackerly, D.D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological monographs*, 80, 401–422.
- Kraft, N.J., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences*, 112, 797–802.
- Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., *et al.* (2016). Plant functional traits have globally consistent effects on competition. *Nature*, 529, 204–207.
- Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E., *et al.* (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters*, 15, 831–840.
- Lanuza, J.B., Bartomeus, I. & Godoy, O. (2018). Opposing effects of floral visitors and soil conditions on the determinants of competitive outcomes maintain species diversity in heterogeneous landscapes. *Ecology Letters*, 21, 865–874.
- Laughlin, D.C. (2014a). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, 17, 771–784.
- Laughlin, D.C. (2014b). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, 102, 186–193.
- Laughlin, D.C., Chalmandrier, L., Joshi, C., Renton, M., Dwyer, J.M. & Funk, J.L. (2018). Generating species assemblages for restoration and experimentation: A new method that can simultaneously converge on average trait values and maximize functional diversity. *Methods in Ecology and Evolution*, 9, 1764–1771.
- Laughlin, D.C., Gremer, J.R., Adler, P.B., Mitchell, R.M. & Moore, M.M. (2020). The net effect of functional traits on fitness. *Trends in Ecology & Evolution*, 35, 1037–1047.
- Laughlin, D.C., Joshi, C., Bodegom, P.M., Bastow, Z.A. & Fulé, P.Z. (2012). A predictive model of community assembly that incorporates intraspecific trait variation. *Ecology Letters*, 15, 1291–1299.
- Laughlin, D.C. & Messier, J. (2015). Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology & Evolution*, 30, 487–496.
- Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16, 545–556.
- Lawton, J.H. (1999). Are there general laws in ecology? *Oikos*, 84, 177–192.
- Li, Y., Jiang, Y., Shipley, B., Li, B., Luo, W., Chen, Y., *et al.* (2021). The complexity of trait–environment performance landscapes in a local subtropical forest. *New Phytologist*, 229, 1388–1397.
- Liu, X. & Rohlf, K. (1998). Impulsive control of a Lotka-Volterra system. *IMA Journal of Mathematical Control and Information*, 15, 269–284.
- Lucia, S., Tăulea-Codrean, A., Schoppmeyer, C. & Engell, S. (2017). Rapid development of modular and sustainable nonlinear model predictive control solutions. *Control Engineering Practice*, 60, 51–62.
- MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101, 377–385.
- Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 97, 199–205.
- Malo, P., Tahvonen, O., Suominen, A., Back, P. & Viitasaari, L. (2021). Reinforcement learning in optimizing forest management. *Canadian Journal of Forest Research*, 51, 1393–1409.

- Marris, E. (2013). *Rambunctious garden: saving nature in a post-wild world*. Bloomsbury Publishing USA.
- Matías, L., Godoy, O., Gómez-Aparicio, L. & Pérez-Ramos, I.M. (2018). An experimental extreme drought reduces the likelihood of species to coexist despite increasing intransitivity in competitive networks. *Journal of Ecology*, 106, 826–837.
- May, R.M. (1973). *Stability and complexity in model ecosystems*. Princeton University Press.
- Mayfield, M.M. & Levine, J.M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093.
- Maynard, D.S., Miller, Z.R. & Allesina, S. (2020). Predicting coexistence in experimental ecological communities. *Nature Ecology & Evolution*, 4, 91–100.
- McCann, K.S. & Gellner, G. (2020). Theoretical ecology: concepts and applications.
- McCarthy, M.A., Possingham, H.P. & Gill, A.M. (2001). Using stochastic dynamic programming to determine optimal fire management for *Banksia ornata*. *Journal of Applied Ecology*, 38, 585–592.
- Monbiot, G. (2015). Meet the ecomodernists: ignorant of history and paradoxically old-fashioned. *The Guardian*.
- Mouillot, D., Loiseau, N., Grenié, M., Algar, A.C., Allegra, M., Cadotte, M.W., *et al.* (2021). The dimensionality and structure of species trait spaces. *Ecology Letters*, 24, 1988–2009.
- Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., *et al.* (2015). Predictive ecology in a changing world. *Journal of Applied Ecology*, 52, 1293–1310.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K. & Ribbens, E. (1996). Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs*, 66, 1–43.
- Palmer, M.A., Ambrose, R.F. & Poff, N.L. (1997). Ecological Theory and Community Restoration Ecology. *Restoration Ecology*, 5, 291–300.
- Pennekamp, F., Iles, A.C., Garland, J., Brennan, G., Brose, U., Gaedke, U., *et al.* (2019). The intrinsic predictability of ecological time series and its potential to guide forecasting. *Ecological Monographs*, 89, e01359.
- Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., *et al.* (2018). Biodiversity increases and decreases ecosystem stability. *Nature*, 563, 109–112.
- Petchey, O.L., Pontarp, M., Massie, T.M., Kéfi, S., Ozgul, A., Weilenmann, M., *et al.* (2015). The ecological forecast horizon, and examples of its uses and determinants. *Ecology Letters*, 18, 597–611.
- Pistón, N., de Bello, F., Dias, A.T., Götzenberger, L., Rosado, B.H., de Mattos, E.A., *et al.* (2019). Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. *Journal of Ecology*, 107, 2317–2328.
- Poorter, L. & Markesteijn, L. (2008). Seedling traits determine drought tolerance of tropical tree species. *Biotropica*, 40, 321–331.
- Pugh, J. (2016). Driven to extinction? The ethics of eradicating mosquitoes with gene-drive technologies. *Journal of Medical Ethics*, 42, 578–581.
- Recht, B. (2019). A tour of reinforcement learning: The view from continuous control. *Annual Review of Control, Robotics, and Autonomous Systems*, 2, 253–279.
- Saavedra, S., Rohr, R.P., Bascompte, J., Godoy, O., Kraft, N.J.B. & Levine, J.M. (2017). A structural approach for understanding multispecies coexistence. *Ecological Monographs*, 87, 470–486.
- Salguero-Gómez, R., Violle, C., Gimenez, O. & Childs, D. (2018). Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. *Functional Ecology*, 32, 1424–1435.
- Scoville, C., Chapman, M., Amironesei, R. & Boettiger, C. (2021). Algorithmic conservation in a changing climate. *Current Opinion in Environmental Sustainability*, 51, 30–35.
- Serván, C.A., Capitán, J.A., Grilli, J., Morrison, K.E. & Allesina, S. (2018). Coexistence of many species in random ecosystems. *Nature Ecology & Evolution*, 2, 1237–1242.

- Shea, K. & Possingham, H.P. (2000). Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. *Journal of Applied ecology*, 37, 77–86.
- Shipley, B., Lechowicz, M.J., Wright, I. & Reich, P.B. (2006). Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology*, 87, 535–41.
- Shoemaker, L.G., Sullivan, L.L., Donohue, I., Cabral, J.S., Williams, R.J., Mayfield, M.M., *et al.* (2020). Integrating the underlying structure of stochasticity into community ecology. *Ecology*, 101, e02922.
- Simberloff, D. (2004). Community Ecology: Is It Time to Move On? (An American Society of Naturalists Presidential Address). *The American Naturalist*, 163, 787–799.
- Simberloff, D. & Stiling, P. (1996). How risky is biological control? *Ecology*, 77, 1965–1974.
- Sonnenburg, J.L. (2015). Microbiome engineering. *Nature*, 518, S10–S10.
- Stein, R.R., Bucci, V., Toussaint, N.C., Buffie, C.G., Räscher, G., Pamer, E.G., *et al.* (2013). Ecological modeling from time-series inference: insight into dynamics and stability of intestinal microbiota. *PLoS Comput Biol*, 9, e1003388.
- Thomas, M.B. (1999). Ecological approaches and the development of “truly integrated” pest management. *Proceedings of the National Academy of Sciences*, 96, 5944–5951.
- Treloar, N.J., Fedorec, A.J., Ingalls, B. & Barnes, C.P. (2020). Deep reinforcement learning for the control of microbial co-cultures in bioreactors. *PLoS computational biology*, 16, e1007783.
- Vellend, M. & Agrawal, A. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, 85, 183–206.
- VENABLE, D.L., PAKE, C.E. & CAPRIO, A.C. (1993). Diversity and coexistence of Sonoran Desert winter annuals. *Plant Species Biology*, 8, 207–216.
- Venturelli, O.S., Carr, A.V., Fisher, G., Hsu, R.H., Lau, R., Bowen, B.P., *et al.* (2018). Deciphering microbial interactions in synthetic human gut microbiome communities. *Molecular systems biology*, 14, e8157.
- Violle, C., Garnier, E., Lecoœur, J., Roumet, C., Pédur, C., Blanchard, A., *et al.* (2009). Competition, traits and resource depletion in plant communities. *Oecologia*, 160, 747–755.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., *et al.* (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.
- Vucic-Pestic, O., Rall, B.C., Kalinkat, G. & Brose, U. (2010). Allometric functional response model: body masses constrain interaction strengths. *Journal of Animal Ecology*, 79, 249–256.
- Wächter, A. & Biegler, L.T. (2006). On the implementation of an interior-point filter line-search algorithm for large-scale nonlinear programming. *Mathematical Programming*, 106, 25–57.
- Wainwright, C.E., Staples, T.L., Charles, L.S., Flanagan, T.C., Lai, H.R., Loy, X., *et al.* (2018). Links between community ecology theory and ecological restoration are on the rise. *Journal of Applied Ecology*, 55, 570–581.
- Warner, R.R. & Chesson, P.L. (1985). Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *The American Naturalist*, 125, 769–787.
- Warton, D.I., Shipley, B. & Hastie, T. (2015). CATS regression—a model-based approach to studying trait-based community assembly. *Methods in Ecology and Evolution*, 6, 389–398.
- Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I. & LeRoy Poff, N. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, 13, 267–283.
- Weiss-Lehman, C.P., Werner, C.M., Bowler, C.H., Hallett, L.M., Mayfield, M.M., Godoy, O., *et al.* (2022a). Disentangling key species interactions in diverse and heterogeneous communities: A Bayesian sparse modelling approach. *Ecology Letters*, 25, 1263–1276.
- Weiss-Lehman, C.P., Werner, C.M., Bowler, C.H., Hallett, L.M., Mayfield, M.M., Godoy, O., *et al.* (2022b). Disentangling key species interactions in diverse and heterogeneous communities: A Bayesian sparse modelling approach. *Ecology Letters*, 25, 1263–1276.
- Widder, S., Allen, R.J., Pfeiffer, T., Curtis, T.P., Wiuf, C., Sloan, W.T., *et al.* (2016). Challenges in microbial ecology: building predictive understanding of community function and dynamics. *The ISME Journal*, 10, 2557–2568.

742 Wisnoski, N.I. & Shoemaker, L.G. (2022). Seed banks alter metacommunity diversity: The interactive
743 effects of competition, dispersal and dormancy. *Ecology Letters*, 25, 740–753.
744 Worthy, S.J., Laughlin, D.C., Zambrano, J., Umaña, M.N., Zhang, C., Lin, L., *et al.* (2020). Alternative
745 designs and tropical tree seedling growth performance landscapes. *Ecology*, 101, e03007.
746 Zhou, J. & Ning, D. (2017). Stochastic community assembly: does it matter in microbial ecology?
747 *Microbiology and Molecular Biology Reviews*, 81, e00002-17.
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For Review Only

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.

772

773 Predictable - the potential for making accurate predictions about a system. High predictability
774 means that the future state of the system can be more readily determined.

775

776 Prediction – a specific, quantitative, and falsifiable statement about the future state of a system.

777

778 Reachable - the potential for obtaining a certain state in the future, given a dynamical model and
779 a current state, and any perturbations applied via a control policy. Not all desired states are
780 necessarily reachable.

781

782 State variable - a variable that describes the current state of the system. Examples include the
783 abundances of the species that are present in (or absent from) the community and the
784 environment.

785

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 $\hat{N}(t_1) = \{N_i(t_1)\}$. Suppose also that the environment is defined by a vector of variables, $\hat{E}(t_1) = \{E_k(t_1)\}$. The goal is to predict or control $\hat{N}(t_2)$ 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 \hat{N} solves a linear system of differential equations:

$$(1) \quad \frac{d\hat{N}(t)}{dt} = \text{diag}(\hat{N}(t))(\hat{r} + A\hat{N}(t))$$

where \hat{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:

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

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

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

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

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

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

810 (6) $\varphi(\hat{E}(t)) = (1 + |\hat{E}(t)|)^{-1}$

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

821

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

823 (7) $r_i(t) = \alpha \hat{T}_i$

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

826

827 **Prediction**

828 Predictions of the future abundance of all species can be determined by numerically integrating

829 $\frac{d\hat{N}(t)}{dt}$. In the GLV case, the fixed point can be found algebraically as (Serván *et al.* 2018):

830 (8) $N_i^* = -A_{ij}^{-1} \times r_i$

831

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

835 (9) $\max(\text{Re}(\{\lambda_i\})) < 0$

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

837

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

840 (10) $\lim_{t \rightarrow \infty} N_i(t) > 0$

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

843

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

847 **Figures**

848 **Figure 1.** Illustration of concepts for predicting or controlling the state of a community. Consider
849 a state space of two species' abundances, N_1 and N_2 along the axes and an initial state (A). **(a)**
850 Predictability measures our ability to know the community's future state. In this example, the
851 community at state A could transition to several future states (B, C, or D) through one or more
852 trajectories each. **(b)** Controllability reflects the possibility of reaching a desired state (here, B,
853 with high abundance of species 1 and species 2). Directly shifting the community to the desired
854 state (purple arrow) may require a high-cost perturbation (either high effort or long time), but
855 one could instead identify a lower cost indirect perturbation (δA , green dashed arrow) to state
856 $A + \delta A$. After this perturbation, the community will reach state B at minimal additional cost. In
857 contrast, no perturbation can reach state E, which is then considered unreachable (infinite cost).

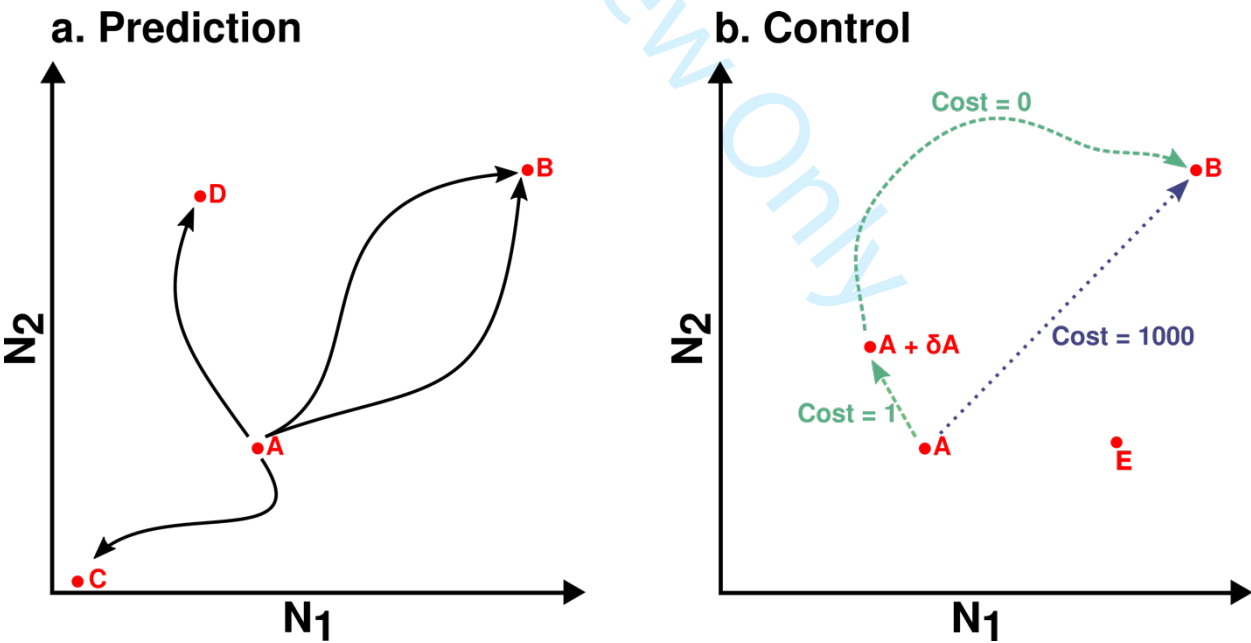
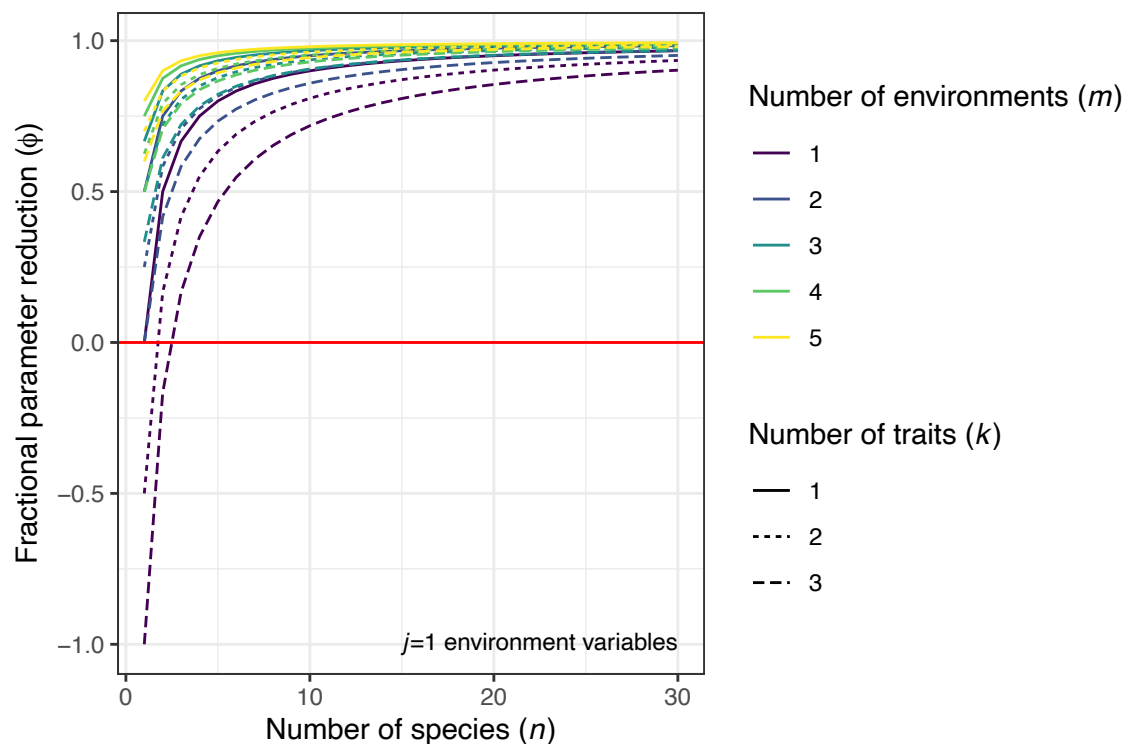
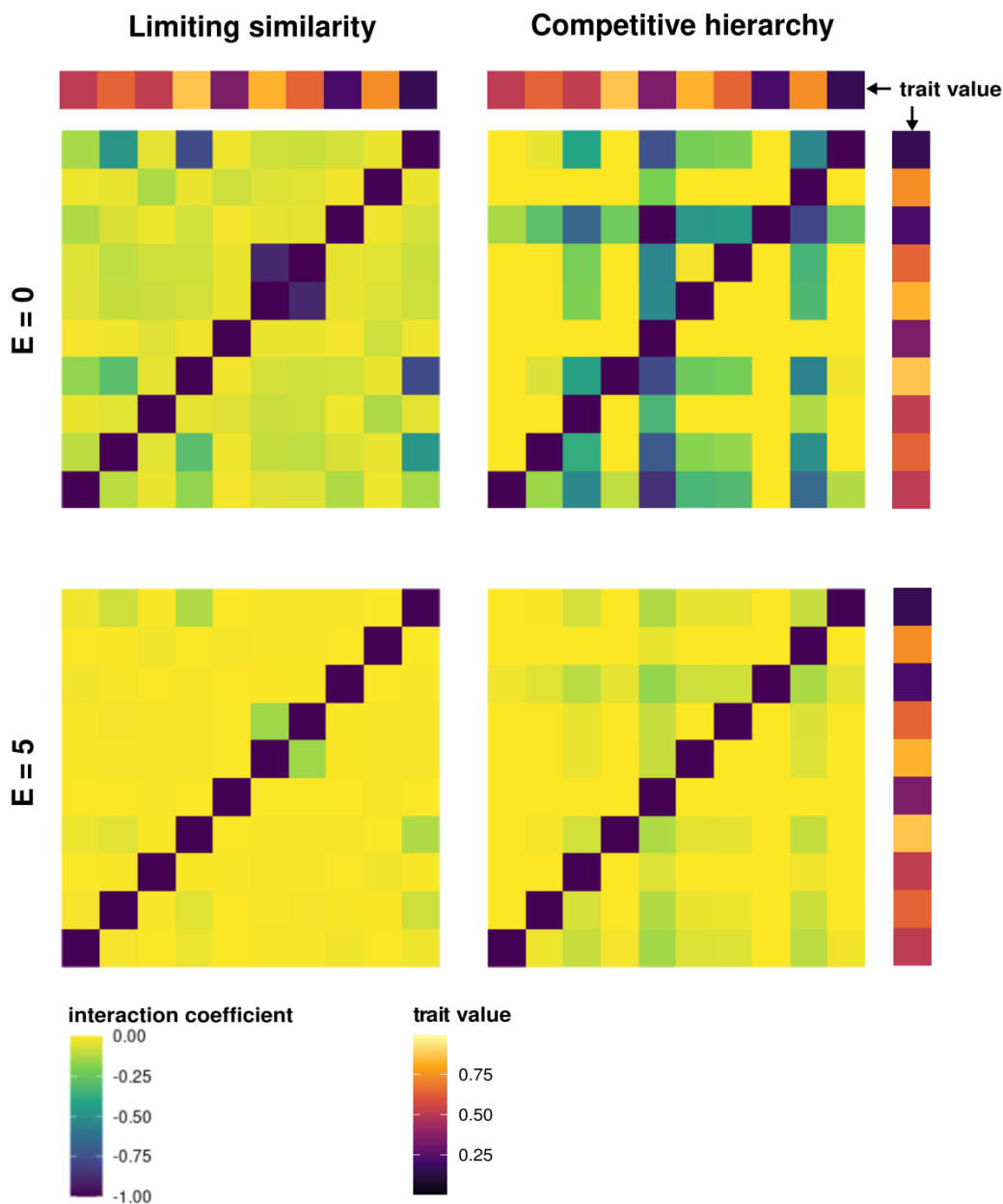


Figure 2. TEMP's can sometimes reduce parameter estimation challenges in the GLV model. The number of parameters needed to use a dynamical model is shown through either (a) direct parameterization or (b) a TEMP. In the GLV model of n species parameterized in each of m discrete conditions, there are $m(n^2 + n)$ free parameters to estimate. Alternatively with the TEMP's 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. (c) The fractional reduction in number of parameters to be estimated, is then $\phi = 1 - (j + nk)/(m(n^2 + n))$. 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's or dynamical models might not yield similar fractional reductions.



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



876

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

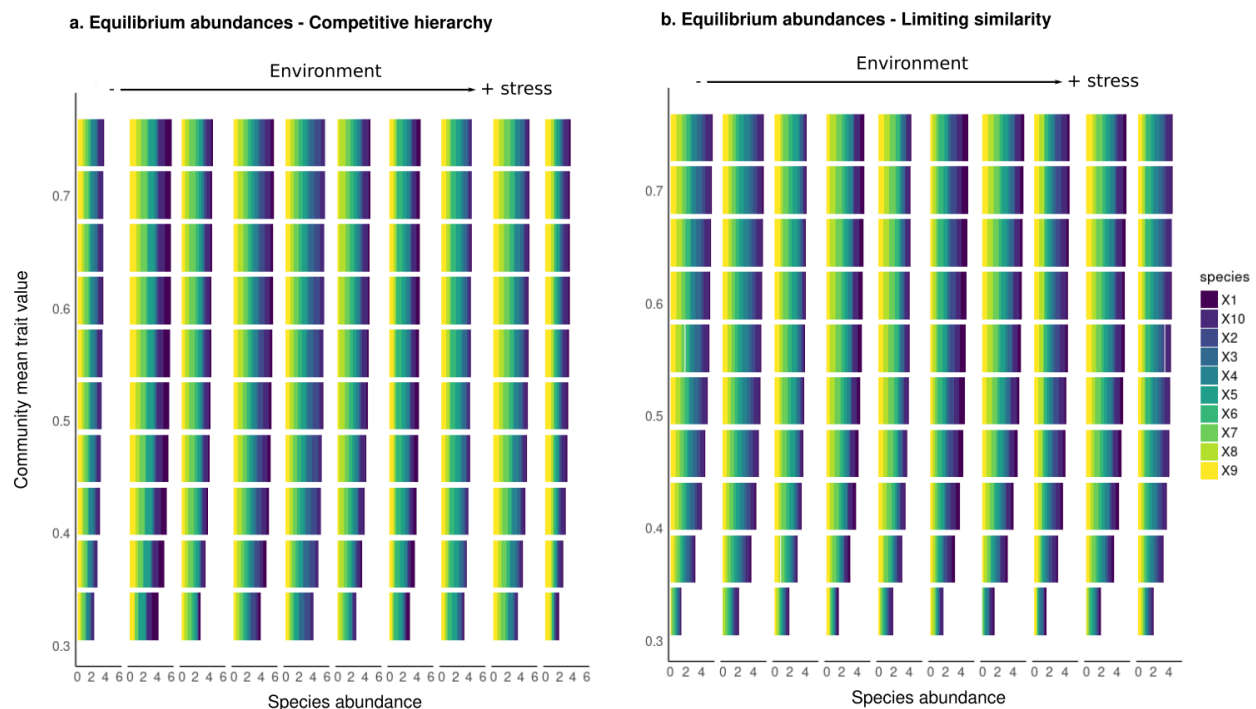


Figure 5. Coexistence outcome predictions for 10-species communities predicted under a competitive hierarchy TEMP (a, b, c) or a normalized limiting similarity TEMP (d, e, f), assuming GLV dynamics. Trait values are sampled from a uniform distribution [0,1] and an environmental gradient [0,1]. Intrinsic 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.

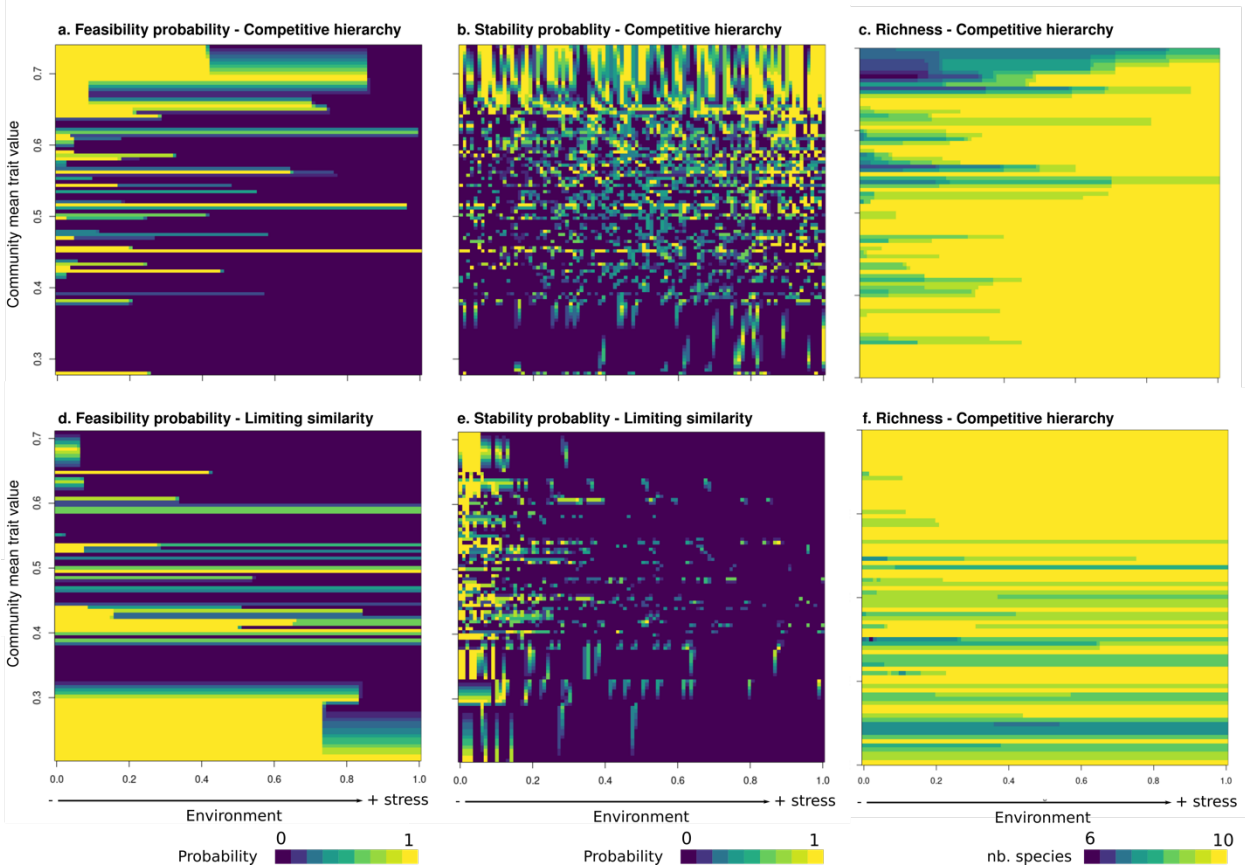


Figure 6. Invasibility surfaces predicted under the hypothesis of **(a)** a competitive hierarchy TEMP and **(b)** a normalized limiting similarity TEMP, both assuming GLV dynamics. Traits for $n=10$ species are sampled from a univariate uniform distribution spanning $[0,1]$ and environment gradient 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 (delineated by a white contour line at 0.0001).

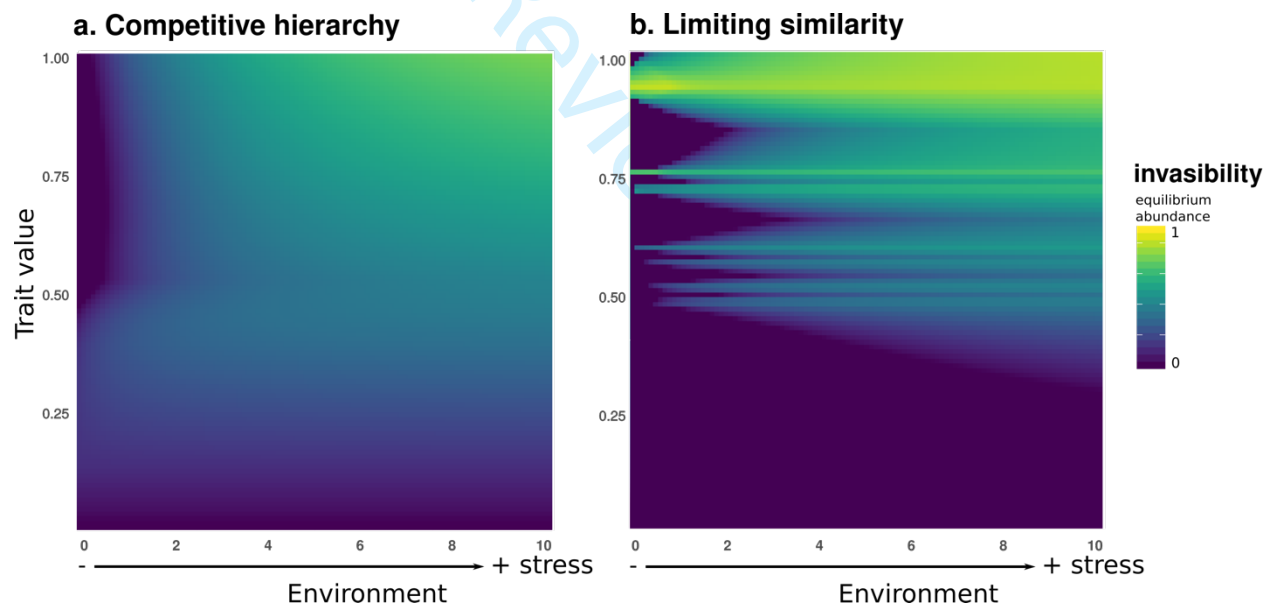


Figure 7. Predictions of trait-environment relationships under a competitive hierarchy TEMP (**a**, **b**) or a normalized limiting similarity TEMP (**c**, **d**), for either linear (**a**, **c**) or periodic (**b**, **d**) environmental change, assuming GLV dynamics. The upper panel shows the temporal 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 $N=0.0005$.

Competitive hierarchy hypothesis

Limiting similarity hypothesis

Linear environmental change

Sinusoidal environmental change

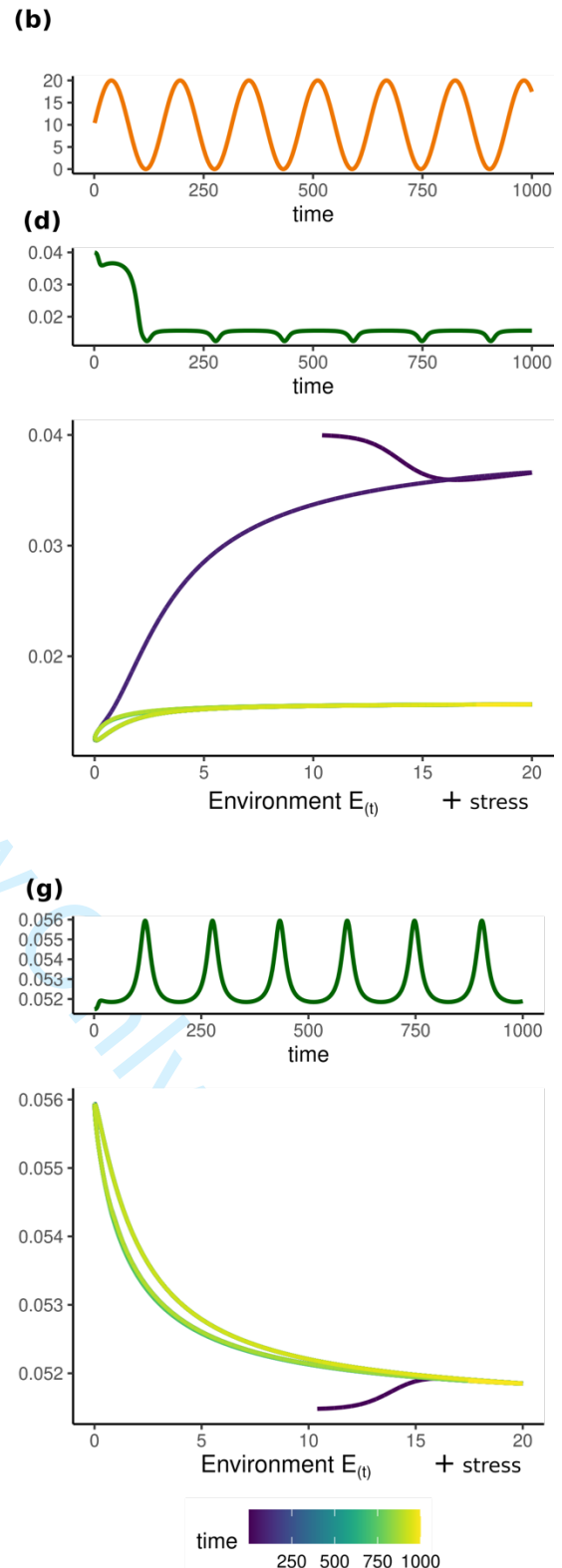
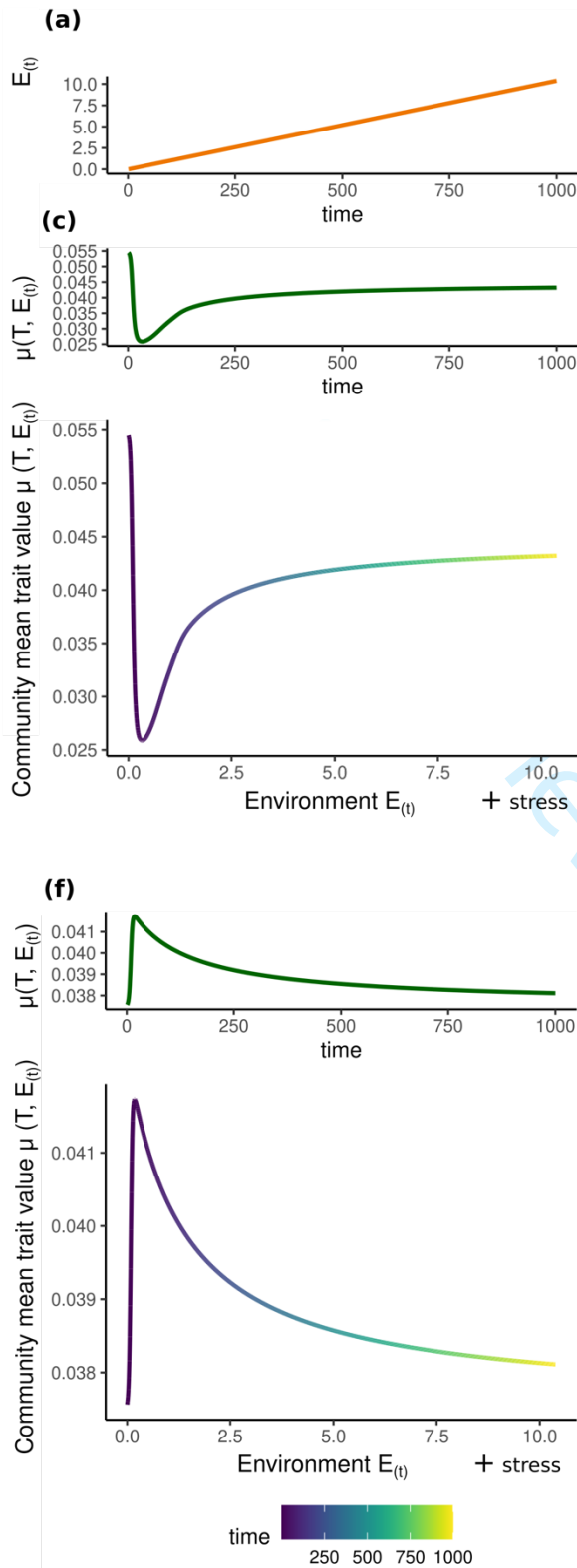


Figure 8. Impulsive control to prevent an unwanted species (*E*) from coexisting in the community by perturbing the environment, assuming GLV dynamics. Traits for $n=10$ species are sampled from a univariate uniform distribution spanning $[0,1]$. Intrinsic growth rates are set constant to $r=0.5$ for 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*.

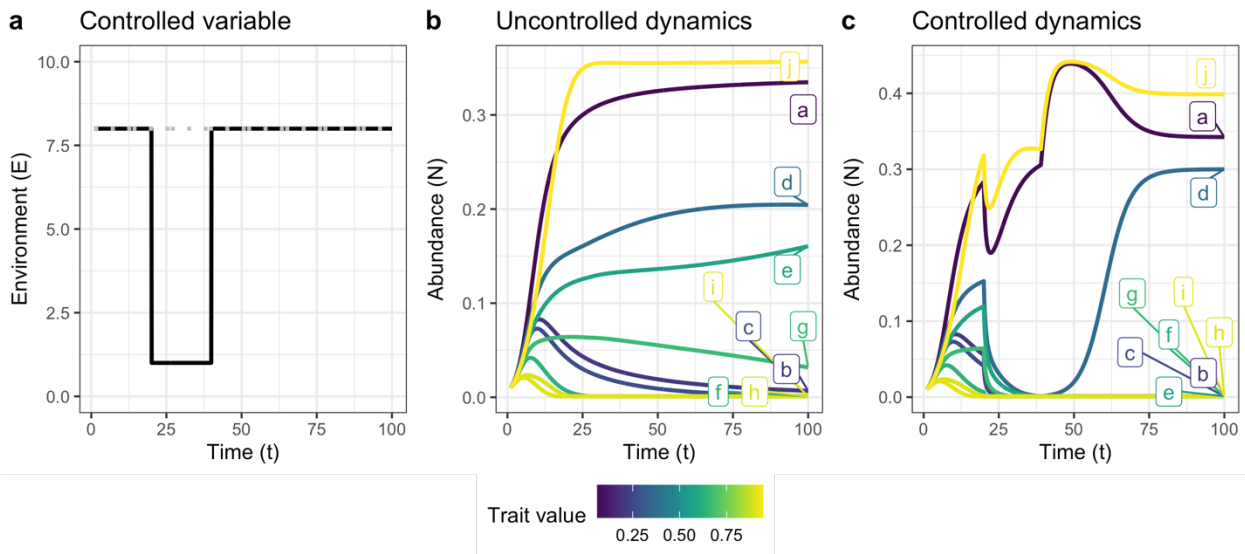


Figure 9. Impulsive control to remove unwanted species and shift species abundances via the introduction of species with certain traits, assuming GLV dynamics. Traits for $n=10$ species are sampled from a univariate uniform distribution spanning $[0,1]$. Intrinsic growth rates are set constant to $r=0.5$ 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.

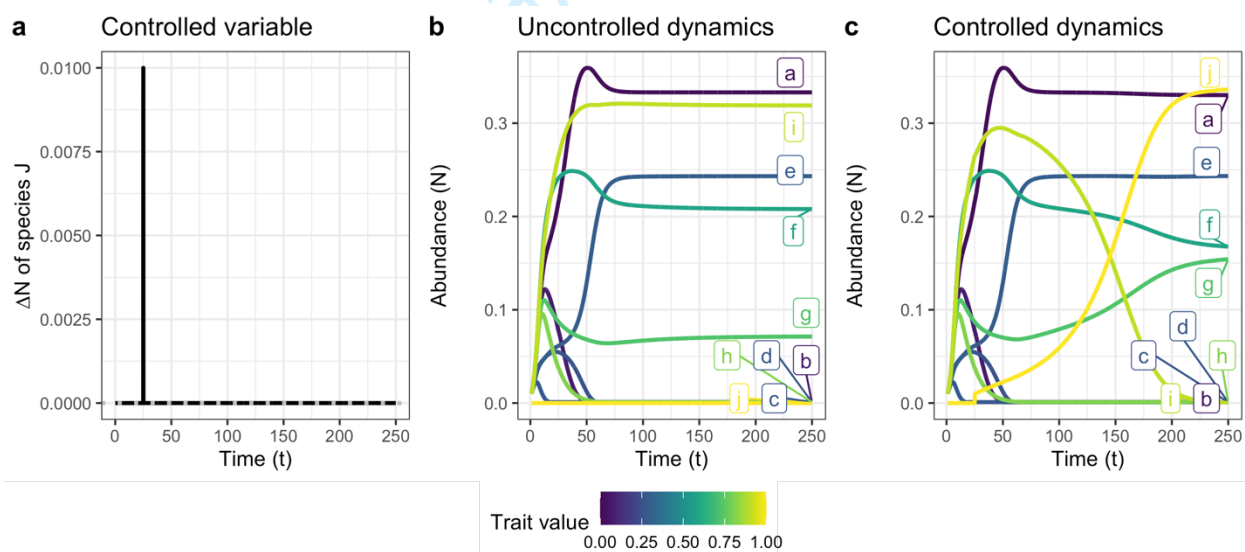
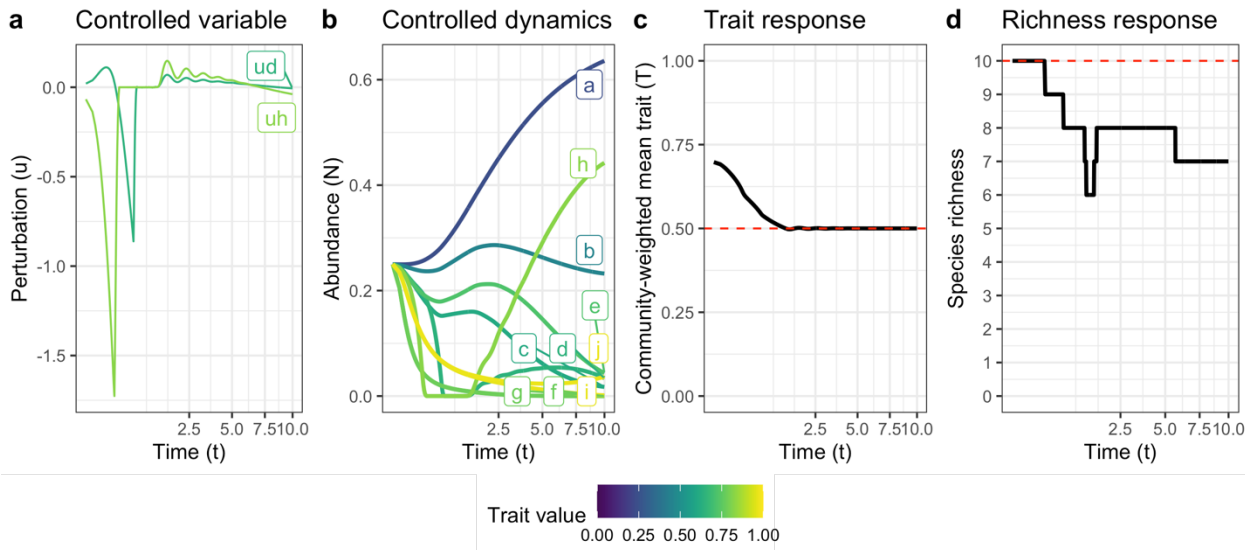
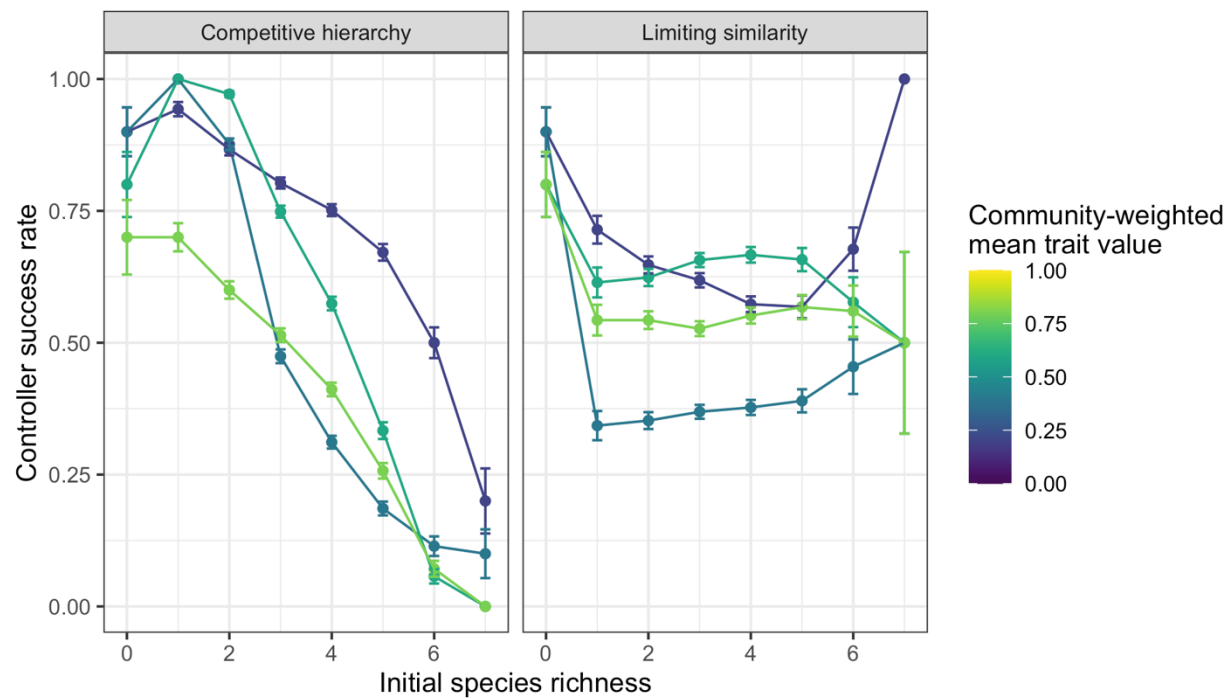


Figure 10. Continuous optimal control to achieve a certain community-weighted mean trait value as a desired state via perturbing the abundances of species with certain traits, assuming GLV dynamics. Traits (T) for $n=10$ species are sampled from a univariate uniform distribution spanning $[0,1]$. Intrinsic 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 **Text S1**.



957 Supporting Information

958 **Figure S1.** Success rate of model predictive control at reaching a target community state with
 959 arbitrary community-weighted mean trait value and maximal richness, based on a TEMP and
 960 assuming underlying GLV dynamics. Panels show success rates for different initial species
 961 richness values and trait-based hypotheses. Confidence intervals indicate distributions of success
 962 rate over different randomly sampled values for species' traits. See Text S1 for details of
 963 simulations.



966 **Text S1.** Description of simulation models and code.

967

968 Reproducibility

969 The code supporting the different sections of the main text can be downloaded from the
970 following repository: **[[BLINDED FOR REVIEW, AVAILABLE TEMPORARILY AS**
971 **SUPPORTING FILE]]**. The repository contains a set of R functions. There is also a script
972 `code_use_paper_figures.R` that can be used as a tutorial to explore the different
973 functions.

974

975 Predicting dynamical model parameters under different TEMPs.

976 The function `predict_demographic_model_parameters.R` computes numerous
977 replicates of interaction matrices from TEMPs under varying parameters combinations: number
978 of species, trait distributions for random sampling of species trait values (Gaussian, uniform,
979 Poisson, bimodal), and different TEMPs (limiting similarity, competitive hierarchy), assuming
980 GLV dynamics. Note that the TEMPs themselves are external functions called by the main
981 function (see `compute_interaction_from_niche_difference.R`,
982 `compute_interaction_from_competitive_dominance.R`). This allows additional
983 TEMPs into the implementation of `predict_demographic_model_parameters.R`.
984 The function returns a data frame (long-format) with all pairs of species from all replicates of all
985 combinations of parameters, corresponding to species' trait values, intrinsic growth rates, and
986 interaction coefficients.

Predicting community dynamics and coexistence outcomes

The function `predict_coexistence_outcome.R` implements predictions of coexistence outcomes. From a set of communities obtained from `predict_demographic_model_parameters.R`, the function assesses coexistence outcomes and properties given the species' A and r parameters in a GLV model implemented as a system of ordinary differential equations (ODE). The function returns:

- coexistence outcomes. The function determines the stability and feasibility of each unique interaction matrix from the analytical study of the ODEs system, and runs numerical simulations of the dynamic system to calculate at the last time step of the simulation t_{max} (number of time steps defined as a function parameter): the equilibrium abundance, the richness of the realized community (number of species with $n_t > N_{min}$ at $t = t_{max}$), the feasibility (i.e all species with $n_t > N_{min}$ at $t = t_{max}$), and the stability (i.e $\delta n_t < N_{min}$ at $t = t_{max}$).
- trait distribution. The function computes statistics of community trait distributions: mean trait value, trait variance, abundance-weighted mean trait value, and abundance-weighted trait variance.
- network properties. The function also computes network properties potentially involved in the coexistence outcomes: three moments (mean, variance, skewness) of the distribution of interspecific interaction coefficients (following (Grilli *et al.* 2017)) the network connectance, modularity, and transitivity.

1009 Predicting invasibility surfaces

1010 The function `predict_invasibility.R` implements invasibility surfaces. In a first step,
1011 for a given set of communities along environmental values computed via
1012 `predict_demographic_model_parameters.R`, the function runs a numerical
1013 simulation for the community dynamic under each environmental value as in
1014 `predict_coexistence_outcome.R` (see above). In a second step, the function introduces
1015 a new invader species at low density (i.e. $N_{min} \times 5$) defined by a given trait value in the simulated
1016 community and re-launches the simulation (from the last time step of the previous simulation)
1017 for a certain number of time steps. For a given invader's trait and environment value, the
1018 invasibility can be interpreted as the equilibrium abundance of the invading species. Performing
1019 invasion simulations on all trait and environment values allows estimation of the invasibility
1020 surface of a community.

1021

1022 Predicting community dynamics in response to environmental change

1023 The function `predict_environmental_change_response.R` implements community
1024 dynamics under temporally varying environment values. We assume that as the environment
1025 changes over time, so also do the dynamical model parameters, following the TEMP of interest.
1026 Temporal variation in the environment can be simulated according to different types of single
1027 events or trajectory (e.g., pulse, step, trend, cyclic) via the function
1028 `simulate_environmental_change.R`. The function returns a 3-element list, with each
1029 list element corresponding to data for each time step:

- The community state. the abundance of each species, the total abundance, the community abundance-weighted mean trait value, community abundance-weighted trait variance, the environment value.
- The Jacobian matrix. At each time step, the Jacobian matrix is estimated numerically from the dynamics.
- The determinant of the Jacobian matrix.

Identify control policies - impulsive control by environment

The file `simulate_impulsive.R` (first half) uses the above functions to set up a community of a given trait composition in a given environment, assuming GLV dynamics and a certain TEMP. An environmental perturbation is proposed over a single interval by trial-and-error. To explore the effects of this environmental change, the community dynamics are simulated over three sequential intervals (before perturbation, during perturbation, after perturbation) during which the environment (and by extension the dynamical model parameters) take different values. The state variables from each time interval are used as inputs for the next time interval.

Identify control policies - impulsive control by species introductions

The file `simulate_impulsive.R` (second half) uses the above functions to set up a community of a given trait composition in a given environment, assuming GLV dynamics and a certain TEMP. An abundance perturbation (species introduction) is proposed at a single time point. To explore the effects of this environmental change, the community dynamics are

simulated over two sequential intervals (before perturbation, after perturbation).

Continuous optimal control by model predictive control

The file `mpc_do.ipynb` replicates the above functions in Python to set up a community of a given trait composition in a given environment, assuming the GLV dynamical model and a certain TEMP. The `do-mpc` toolbox for model predictive control is then used to identify optimal control policies. The file specifically explores a case where the species abundance can be perturbed. In this case, all the parameters are constant in time and the community dynamics equation is modified to be:

$$(Eq. S1) \quad \frac{d\hat{N}(t)}{dt} = \text{diag}(\hat{N}(t))(\hat{r} + A\hat{N}(t)) + B \cdot \hat{u}(t)$$

Where B is a $n \times 1$ binary matrix whose non-zero entries indicate the controllable state variables and $\hat{u}(t)$ is a $n \times 1$ binary matrix whose entries indicate the abundance perturbations of each state variable over time. The ‘.’ notation indicates elementwise multiplication. The abundances of species are initialized to their equilibrium abundances following **Box 2**. The objective function J is set to minimize the distance between the current community weighted mean trait composition (\bar{T}) and a target value (\bar{T}_{target}) and maximize the total richness (S), where

$$(Eq. S2) \quad \bar{T} = (\sum_i T_i N_i) / (\sum_i N_i)$$

$$(Eq. S3) \quad S = \sum_i (N_i > 0.001)$$

$$(Eq. S4) \quad J = \sum_{j \in n_{horizon}} (\bar{T} - \bar{T}_{target})^2 / (S + 0.1) + \Delta u_j^T R_j \Delta u_j$$

where the T superscript indicates transposition, and R penalizes the magnitude of change in the input to encourage convergence to an autonomous or input-stabilized fixed point. The additional

factor of 0.1 in the denominator is included to prevent convergence issues if S reaches 0. Different forms for **Eq. S4** could yield different outcomes (e.g. via differential weighting of the first and second terms, or treating the numerator and denominator in the first term additively instead of multiplicatively) that we did not explore in this illustrative study.

The problem (minimize J for the dynamics of **Eq. S1** over the possible inputs and state trajectories) is then solved using a closed-loop controller that operates over a total interval of 1000 timesteps of 10^{-2} each, also with a 10^{-3} factor penalty on the total magnitude of the perturbations, where $n_{horizon} = 3$, and subject to state and input constraints

(Eq. S5) $N_i \in [10^{-8}, 5], u_i \in [-10, 10]$.

We assume that B is 0, except for on the diagonal elements corresponding to the dimensions that are considered perturbable – in this case, for the two species with the minimum and maximum traits and 0 otherwise.

The problem is solved in python with the *do-mpc* package, which utilizes the *CasADi* and *IPOPT* solver (Wächter & Biegler 2006; Lucia *et al.* 2017; Andersson *et al.* 2019). The optimal trajectory is found by integrating the true, nonlinear dynamics by orthogonal collocation of finite elements (Biegler 2010). Computation requires approximately one second on a contemporary laptop computer.

Success rate of continuous optimal control

1092 To extend the above simulation to a comprehensive analysis of performance,
1093 `traitMPC_stats_final.py` shows that the proposed GLV model with a TEMP can often
1094 be driven to arbitrary targets (**Fig. S1**).

1095
1096 We repeat the above analysis, specifying arbitrary trait targets (from $\bar{T} = 0.2$ to $\bar{T} = 0.8$ in steps
1097 of 0.2, for initial species compositions ranging from $n=0$ to $n=7$ species. Initial compositions
1098 include all the $2^7 = 128$ stable and feasible fixed points of varying richness of the GLV model.
1099 Simulations are replicated for 10 replicate samples of species' traits from a uniform distribution
1100 $U(0,1)$, as in the main text, and with $E=8$.

1101
1102 In each case, the optimal control program is solved iteratively for a maximum time of 10
1103 computation hours during which the dynamics are progressed with the first input in the solution
1104 at each time step $\Delta t = 0.1$. The iterations are halted if the controller has converged, defined by
1105 the boundedness of the L_1 norm of $\partial N / \partial t$ and $\partial^2 N / \partial t^2$ for 25 of the last 50 time steps. Success
1106 is defined as the controller's ability to converge before the maximum computation time to a point
1107 of at most 0.1 distant from the target.

1108
1109 For a variety of target trait compositions, initial species richness values, and both the limiting
1110 similarity and competitive hierarchy TEMP, success is achieved at high rates (**Fig. S1**). The
1111 MPC often succeeds despite only two of the species being controlled from a variety of initial
1112 points spanning initial richness. In both TEMPs, the trend is that lower target trait compositions
1113 result in higher success. Given that the weights are randomized between 0 and 1, the value of the
1114 trait composition is bounded by the minimum and maximum trait values. These are only

1115 achieved when the maximum or minimum corresponding dimension is at high abundance.
1116 However, this is confounded by the objective to both include as many species as possible
1117 (normalization to richness penalty) and find an equilibrium (change of input penalty).

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