



Theoretical guidelines for editing ecological communities

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ABSTRACT

Having control over species abundances and community resilience is of great interest for experimental, agricultural, industrial and conservation purposes. Here, we theoretically explore the possibility of manipulating ecological communities by modifying pairwise interactions. Specifically, we establish which interaction values should be modified, and by how much, in order to alter the composition or resilience of a community towards a favorable direction. While doing so, we also take into account the experimental difficulties in making such modifications by including in our optimization process, a cost parameter, which penalizes large modifications. In addition to prescribing what changes should be made to interspecies interactions given some modification cost, our approach also serves to establish the limits of community control, i.e. how well can one approach an ecological goal at best, even when not constrained by cost.

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1. Introduction

Controlling ecological communities has so far had mixed success. Since the population dynamics of a community can sensitively depend on the precise values of interactions and species abundances, attempts motivated by qualitative reasoning has led to ineffective control of targeted species or adverse outcomes on untargeted species (Hoddle, 2004; Louda and Stiling, 2004; Messing and Wright, 2006; Schlaepfer et al., 2011; Van Driesche et al., 2010). An engineer can design a complex electronic device on the drawing board before building a fully functioning prototype. Can an ecologist design communities in a similar way? Our aim here is to develop analytical methods that might serve as a guide for manipulating the composition and resilience of communities.

In the literature we see two types of problems that motivate such quantitative approaches. The first problem concerns eradicating invasive species and pests, typically by releasing natural enemies as control agents or directly culling pests. These studies are limited to few-species or few trophic levels such as prey and predator (Jiang and Lu, 2007; Jiang et al., 2007; Liu et al., 2006; Liu and Chen, 2003; Zhang et al., 2016), prey, predator, and the predator's predator (Baek, 2010), one predator and multiple prey (Georgescu, 2011), one prey and multiple predators (Pei et al., 2005), and two prey and two predators (Rafikov et al., 2008). These control schemes employ feedback response, require frequent mea-

surements of abundances, and therefore are challenging to implement even for small communities.

The release of parasitoids as a biological control agent can avoid the continuous or periodic interventions required by feedback schemes. As reviewed by Waage and Hassell, 1982 and Van Lenteren, 1983 routine applications of pesticide aided the release of biological control agents, and researchers historically considered both control mechanisms together. However, the short-term economic gains offered by pesticides have caused them to dominate the market of ecological management (Carvalho, 2006; Carvalho, 2017). Research is now focusing back on biological control agents as a means to reduce the world's reliance on chemical controls (Bale et al., 2008) due to the wide range of environmental, ecological, and health impacts of chemical control agents on a global scale (Talebi et al., 2011; Abrol and Shankar, 2014; Rosic et al., 2020). However, the release of parasitoids as a biological control agent is not absent of adverse effects (Pearson and Callaway, 2003). Although parasitoids have a high specificity towards their intended host, some have also been known to attack non-target arthropods similar to their host and compete with native parasitoids (Taylor, 1979; Brodeur and Rosenheim, 2000; Gerling et al., 2001; Garipey et al., 2008; Zappala et al., 2012; Hepler et al., 2020). Clearly, it is essential to consider the effects of such control schemes on non-targeted species in local or regional ecological communities.

The second type of control problem concerns controlling species abundances for industrial purposes. Chemostat models offer a tightly-controlled environment with a low number of interacting species. These reactors can be optimized for maximal production

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rate of useful biological byproducts (Yang and Tang, 2019; Sun et al., 2011; Wei et al., 2013; Cheng et al., 2012; De and Smith, 2003). A consumer-resource model can be used to optimize pH, influx, and dilution rates for production (Girard et al., 1999). This production step is often the starting point for further purification and optimization for commercial use (Blakney et al., 2021).

While it is much more feasible to monitor species abundances and implement precise control curves in a chemostat, these communities are also relatively simple, since in such uniform environments the principle of competitive exclusion eliminates all but few of the species (Sommer, 1983; Xu and Yuan, 2016). More sophisticated chemostat models have been proposed (Mazenc and Jiang, 2009; Mazenc and Malisoff, 2012) which restricts the growth rates or introduces additional nutrients in order to sustain multiple species.

At the intermediate scale are control applications in greenhouses. At this scale, biological agents have been widely used to limit pests to maximize economic output (Paulitz and Bélanger, 2001). This type of environment offers a good balance between community size and controllable parameters. For example, greenhouses can be used to determine species interactions based on functional traits (Caruso et al., 2020). Furthermore, greenhouse control problems have been widely examined in the context of parasitoid control agents targeting insect pests (Nonomura and Toyodaonmura and Toyoda, 2020). The accessibility to community environmental parameters like light exposure, temperature, and humidity promotes the usage of greenhouses as excellent, medium-scale communities to study various control schemes (Fernández et al., 2021). In the context of control, temperature and light exposure can be used to optimize greenhouse output (Jones-Baumgardt et al., 2020; Tang et al., 2020).

Fully examining large-scale ecological communities has historically been very difficult due to limited data. Typically these studies focus on quantitative descriptions of interactions (Sih et al., 1985; Bouskila, 1995; Singh et al., 2009), and field studies can be both difficult and expensive to implement (Lemoine et al., 2016). For these reasons, the control of large ecological communities has been focused on limiting the study focus to a subset of species. For example, empirical studies have been done for two to five species (Snyder et al., 2008; Tonnang et al., 2009; Friman et al., 2014; Royauté and Pruitt, 2015; Chalmandrier et al., 2021). This limited size allows for a detailed analysis of various control schemes through more complex analytical models (Jiang and Lu, 2007; Jiang et al., 2007; Liu et al., 2006; Liu and Chen, 2003; Zhang et al., 2016). However, these local communities are embedded into a large ecological system, and the ignorance of this coupling can be dangerous when the control schemes are transferred to larger communities. Empirical examples of this pitfall have been well documented in history as unintended consequences of ecological controls on non-targeted species (Council, 1996; Hoddle, 2004).

Additionally, there are several cases where the non-native generalist predator control agent escalated the initial threats and lead to the extinction of native species (Louda and O'brien, 2002; Hays and Conant, 2007; Shanmuganathan et al., 2010). Overall, ecological control problems are complex due to the limited availability of data on the interactions between species. A robust analytical framework that can assess control consequences when scaling up to large communities can help address non-targeted effects and hopefully mitigate unintended effects.

An ideal ecological control theory must be scalable: the control procedure should not sensitively depend on the size or the complexity of the community. It should work for a diverse variety of trophic structures. It should also be experimentally feasible: it should not require harvesting or breeding control species in real time according to precise curves, or require continuous monitoring the abundances of many species.

Here we explore the possibility of making a one-time change in an ecological community in order to shift its equilibrium composition towards a desirable target, or increase its resilience. Our framework consists of identifying the ideal attributes of a “control species”, which, when introduced into the community once, will permanently alter its composition or stability.

Experimentally, there are multiple potential ways to modify a community interaction matrix. Genes and transcription factors that modulate interspecies interactions can be targeted through gene editing (Tétard-Jones et al., 2007; MMooney and Agrawal, 2008; Broekgaarden et al., 2008; Whitham et al., 2012; Abdala-Roberts et al., 2012; Lamit et al., 2015). If the strain with the new interaction is more fit, it will naturally invade. If not, the original strain must be annihilated first so that the engineered strain can fill its niche. Second, one could make use of the diversity of interaction values already present in a population (for example, some predators may already be better at catching prey) (Mooney, 2011; Barker et al., 2018; Zytynska et al., 2019). In this case, one would isolate an individual with the desirable interaction value, culture it, and add it back to the original community in much larger numbers. Interaction values can also be modified by environmental factors such as temperature, pH, and chemicals (Tylianakis et al., 2008; Englund et al., 2011; Rall et al., 2012; Sentsis et al., 2012; Griffiths et al., 2015; Ratzke and Gore, 2018; Mugabo et al., 2019; Niehaus et al., 2019). For example one could use a drug that targets a protein responsible for mediating a particular interspecies interaction.

Despite these possibilities, engineering species with desired interaction properties presents many technical challenges. As interesting as these challenges are, here we fully omit the problem of actually *building* control species and instead focus on the problem of *designing* control species, –just as an engineer might overlook how circuit elements are actually manufactured and focus on the design of a circuit. Furthermore, our goal here is to determine the characteristics of the *ideal* control species, even though a real species, natural or engineered, might be a mere approximation of this ideal, – just as real circuit elements are approximations of ideal ones.

Problem Statement. We will work with the generalized Lotka-Volterra equations, which describe the population dynamics of sparse, well-mixed communities

$$\dot{n}_i = n_i \left(r_i + \sum_{j=1}^N A_{ij} n_j \right) \quad (1)$$

where the abundance $n_i(t)$ of species i changes according to its intrinsic growth rate r_i and its interactions with others A_{ij} .

The Lotka-Volterra model has been used to describe communities of varying scales. These equations have good agreement with empirical data for parasitoid and host behavior (Tonnang et al., 2009; Margiotta et al., 2017), inferring interactions greenhouse communities (Dormann, 2007; Téllez et al., 2020), and multi-trophic descriptions of food webs (Carrara et al., 2015; Mühlbauer et al., 2020). The simple linear functional response provides a good trade-off between predictive power (matching empirical data) and analytical complexity (more detailed functional responses).

The goal of this study is to solve the following three problems (Fig. 1). **(1)** Modify an interaction matrix element such that the equilibrium community composition shifts towards a new desirable state. **(2)** Modify an interaction matrix element so that a latter random change influences the community composition minimally. **(3)** Add a novel species (a new row and column to the interaction matrix) to shift the community composition towards a new desirable state. While addressing these problems, we will also establish theoretical limits to community control: we will determine how

much one can vary the composition and resilience of a community at best, even if one could introduce arbitrarily large changes to the interaction values.

The coexistent equilibrium of Eqn. (1), $\vec{n} = \vec{x} = -\mathbf{R}\vec{r}$, is obtained by setting the parenthesis to zero (provided that $\mathbf{R} \equiv \mathbf{A}^{-1}$ exists and $x_i > 0$). For our purposes, we assume that our system originally resides in a coexistent state in stable equilibrium. As we will see, our control protocols will largely succeed in maintaining both the stability and coexistence, however this is not guaranteed.

Model Assumptions. In summary, our framework assumes that the conditions that allow the use of the Lotka-Volterra equilibrium hold true. The Lotka-Volterra model is one of the staples of population dynamics and its domain of applicability is well-established (Arthur, 1969; O’Dwyer, 2018). These conditions, briefly stated, are: (1) The community consists of well-mixed species whose abundances are large enough to neglect stochastic noise, but small enough that the time it takes to process prey is shorter than that it takes to run into new prey. (2) The rate at which abundances fluctuate is faster than the rate at which interspecies interaction values evolve. i.e. we assume that community control takes place within time scales slower than that required for evolutionary arms races between species. (3) The system starts near a stable equilibrium, and as we gradually shift this equilibrium point, it continues to retain its stability.

2. Methods

Our main results consist of general analytical formulas. However we verified and illustrated these formulas with specific simulated communities. In the simulations, we first construct anti-symmetric ($A_{ij} = -A_{ji}$) matrices with normally distributed values with mean $\langle A \rangle = 0$ and variance $\sigma_A^2 = 1$, then reduce all positive interaction values by a factor of $\eta = 10$ to account for mass transfer inefficiency. We set the diagonal values to $A_{ii} = d = -1$, since most species are self-limited by intraspecific competition (Chesson, 2000; Adler et al., 2018). Then, we generated normally distributed equilibrium abundances x_i with average $\langle x \rangle = 1$ and variance $\sigma_x^2 = 10^{-2}$, making sure $x_i > 0$. Note that A and x determine the growth rate vector according to the coexistent equilibrium condition $\vec{r} = -\mathbf{A}\vec{x}$. Then we discarded all communities for which x was an unstable equilibrium. To gather statistics we generated 100 random communities and 100 random targets for scheme 1, and 1000 communities and 1000 random targets for the computationally-cheaper scheme 3. We chose $\zeta = 10^{-3}$ for scheme 2 and gather statistics over 1000 communities.

For the community size we picked $N = 20$ (unless varied in a plot) since communities larger than this tend to be unstable for our parameter values. For the intrinsic growth rate for the control species we always set $v = 1$. When determining a target towards which the abundances are to be steered, we pick a random direction, but fix its distance at $|\vec{u}| = 2$.

3. Results

Control scheme 1: Interaction modification for displacing equilibrium abundances. Our first control scheme involves modifying the interaction between two species in order to move the original equilibrium composition \vec{x} as close as possible to a desirable target \vec{y} .

A change in a single matrix element $A_{ab} \rightarrow A_{ab} + \epsilon$ leads to a change in its inverse $\mathbf{R} \rightarrow \mathbf{R}'$. We use the Woodbury matrix identity to find

$$R'_{ij} = R_{ij} - \epsilon \frac{R_{ia}R_{bj}}{1 + \epsilon R_{ba}}. \tag{2}$$

Upon modifying the matrix element, the equilibrium composition becomes

$$\vec{z} = -\mathbf{R}'\vec{r} = \vec{x} - \mu\vec{w}_a \tag{3}$$

where \vec{w}_a is the a^{th} column of \mathbf{R} and $\mu = \epsilon x_b / (1 + \epsilon R_{ba})$. This tells us that the equilibrium can be displaced along only certain directions \vec{w}_a , indexed by $a = 1, 2, \dots, N$. If the desired target is along one of these directions then we can hope to reach it precisely. Otherwise, the best we can do is to come close.

We will find which interaction matrix element should be modified, and by how much, by minimizing

$$\mathcal{L} = |\vec{y} - \vec{z}|^2 + \alpha\epsilon^2. \tag{4}$$

The first term ensures that we come close to our target, while the second term accounts for the difficulty in making changes to interspecies interactions. α , the only adjustable parameter in this scheme, is the modification cost per modification. It quantifies the relative importance of making small changes versus approaching our target. The smaller the cost, the larger our modification can be, and the closer we can approach our target.

We should caution that for sufficiently large perturbations, $\epsilon \rightarrow -1/R_{ba}$, Eqn. (2) blows up. Such changes will destabilize the community and collapse it into a smaller one after a cascade of species extinctions. Dealing with this singularity is mathematically challenging, and for the most part practically undesirable, so most analytical results here concern with perturbations that are far away from this singularity. Specifically, we will focus on the “large” α regime (leading to small perturbations that fall short of hitting the singularity) and the small α regime (leading to large perturbations pushing us beyond the singularity).

To minimize \mathcal{L} we solve for ϵ^* that satisfies $\frac{d\mathcal{L}}{d\epsilon}|_{\epsilon^*} = 0$. Taking the derivative and reorganizing terms, we get

$$\epsilon^* = \gamma / [\alpha(1 + \epsilon^* R_{ba})^3 - \beta] \tag{5}$$

$$\gamma = -x_b \vec{u} \cdot \vec{w}_a, \quad \beta = R_{ba} \gamma - x_b^2 |\vec{w}_a|^2, \quad \vec{u} = \vec{y} - \vec{x}.$$

Eqn. (5) is a quartic polynomial with an exact analytical solution shown in Fig. 3. Since the analytical formula for this solution is

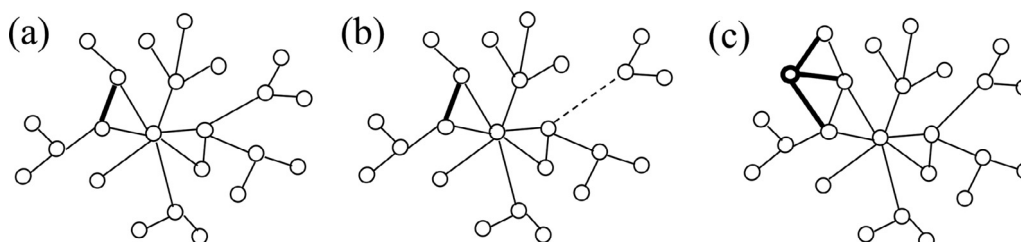


Fig. 1. Three control schemes for editing ecological communities. (a) Modifying an interaction (bold) to displace equilibrium abundances. (b) Modifying an interaction (bold) to reduce displacements caused by a random latter change (dashed). (c) Adding an exogenous species with tailored interactions (bold) to displace equilibrium abundances.

rather lengthy, we omit it here and simply refer to (Weisstein, 2020).

Now we focus on the special cases of large and small α , which will be useful as we move on, as well as biologically more insightful. We start by observing that Eqn. (5) has ϵ^* both on the right and left side, which we arranged in this way to solve for ϵ^* perturbatively. For $\alpha \rightarrow \infty$, we have $\epsilon^* = 0$. For large but finite costs, we can plug in $\epsilon^* = 0$ to the right, and get $\epsilon^* = -\gamma/(\beta - \alpha)$ on the left. Then we repeat, plugging this into the right, to get

$$\epsilon^* \simeq \frac{\gamma}{\alpha[1 - \gamma R_{ba}/(\beta - \alpha)]^3 - \beta} \quad (\text{Large } \alpha \text{ limit}) \quad (6)$$

on the left. This procedure very rapidly converges to the true solution, and our numerical tests show that Eqn. (6) is already quite accurate for practical purposes.

We follow a similar procedure for small costs. For $\alpha \rightarrow 0$, Eqn. (5) gives $\epsilon^* = -\gamma/\beta$. For small but non-zero costs, this solution can be plugged back to the right side of Eqn. (5),

$$\epsilon^* \simeq \frac{\gamma}{\alpha(1 - \gamma R_{ba}/\beta)^3 - \beta} \quad (\text{Small } \alpha \text{ limit}) \quad (7)$$

Note that the second order approximations Eqns. (6) and (7), as well as their first order analogues overlap for $\alpha \rightarrow 0$ and $\alpha \rightarrow \infty$, but depart for intermediate values. Fig. 3 compares these asymptotic forms with the exact analytical solution of Eqn. (5). In all panels, we take the root of the equation corresponding to the global minimum of the quartic polynomial.

Eqns. (6) and (7) prescribe the ‘‘best bang for the buck’’ amount of change that must be introduced to A_{ab} for a particular pair (a, b) , for large and small costs. But there are N^2 pairwise interactions, and thus N^2 optimal ϵ^* 's. Which (a, b) pair is the best to modify?.

Ideally, we should substitute ϵ^* into Eqn. (4) for all (a, b) , and identify the (a, b) that minimizes \mathcal{L} . However, we outline an easier and more insightful way to obtain the best (a, b) for small and large costs. We start by writing Eqn. (4) as,

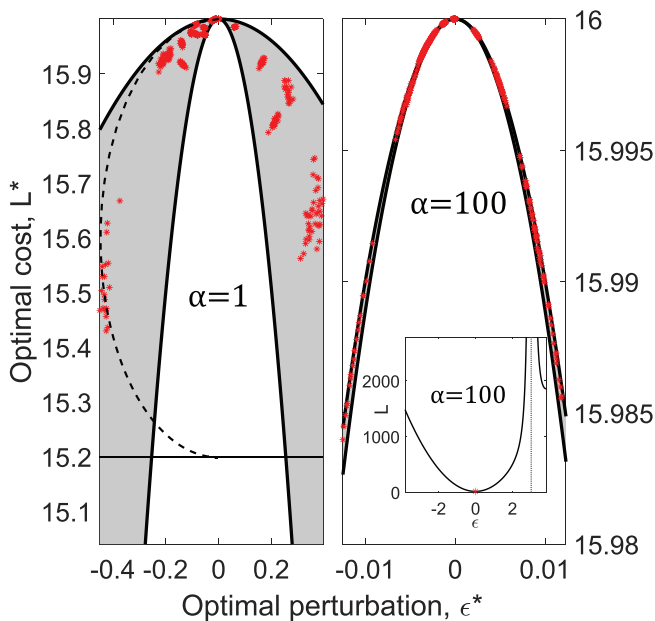


Fig. 2. Control scheme 1: Optimal perturbation to a single A_{ab} for all a, b . Each red dot is the global minimum of \mathcal{L} as obtained from the exact analytical solution to Eqn. (5) for a given (a, b) pair. Eqn. (10) is used to sweep across pairs (a, b) for the n^2 parabolas (grey), which are bound between two special parabolas (black). The thin horizontal line shows the limit as $\alpha \rightarrow \infty$ for the best \vec{w}_a . The inset shows the cost function for the best (a, b) with the singularity marked by a vertical line. For system parameters cf. Methods.

$$\mathcal{L}(\epsilon) = u^2 + \frac{x_b^2 |\vec{w}_a|^2 \epsilon^2}{(1 + \epsilon R_{ba})^2} - \frac{2\epsilon\gamma}{1 + \epsilon R_{ba}} + \alpha \epsilon^2. \quad (8)$$

In the large α limit ($\epsilon^* \rightarrow \gamma/(\alpha - \beta)$ and $\alpha \gg \gamma R_{ba}$),

$$\mathcal{L}^* = u^2 - \gamma^2/(\alpha + w_a^2 x_b^2) = u^2 - x_b^2 (\vec{u} \cdot \vec{w}_a)^2 / (\alpha + w_a^2 x_b^2) \quad (9)$$

As we see, to minimize this, we must simply pick the b corresponding to the species with largest abundance x_b and the a that maximizes the dot product $\vec{u} \cdot \vec{w}_a$. Both of these conditions make biological sense.

The collection of all species interactions (a, b) , define a large number of parabolas, plotted gray in Fig. 2. Interestingly, these parabolas are bounded above by $\mathcal{L}^* \approx |\vec{u}|^2 - \alpha \epsilon^{*2}$ and below by $\mathcal{L}^* \approx |\vec{u}|^2 - (\alpha + x_{\max}^2 w_{\max}^2) \epsilon^{*2}$ where x_{\max} is the largest population abundance and w_{\max}^2 is the displacement vector with the largest norm. These bounds are shown in Fig. 2 and can be readily obtained by writing γ in terms of ϵ^* using Eqn. (5),

$$\gamma = [\alpha(1 + \epsilon^* R_{ba})^3 + x_b^2 |\vec{w}_a|^2] \frac{\epsilon^*}{1 + \epsilon^* R_{ba}}$$

and then plugging this into Eqn. (8),

$$\mathcal{L}^* \approx |\vec{u}|^2 - (\alpha + x_b^2 w_a^2) \epsilon^{*2}. \quad (10)$$

Now we turn to the $\alpha \rightarrow 0$ limit ($\epsilon^* \rightarrow -\gamma/\beta$), where Eqn. (8) gives

$$\mathcal{L}^* = u^2 + \gamma^2 \left(\frac{\alpha}{\beta^2} - \frac{1}{w_a^2 x_b^2} \right) \simeq u^2 (1 - \cos^2 \theta_a). \quad (11)$$

Here θ_a is the angle between \vec{u} and \vec{w}_a . This tells us that when the controller is not constrained by cost, they should simply pick the displacement vector \vec{w}_a best aligned with the desired displacement direction and then they could modify any element b .

The large- α result emphasized the effectiveness of small modifications which required taking advantage of species with large population abundances and strong displacement magnitudes to more easily propagate our perturbation. In this regime, however, interaction cost does not matter and the only restriction is based on the natural displacement directions of the community.

The inset in Fig. 2 shows a numerical example where Eqn. (6) minimizes \mathcal{L} . Each red star in the left and right panels of Fig. 2 is such an optimal solution for different (a, b) pairs. Most interaction modifications do not effectively shift the abundances towards our target \vec{y} but there exists a couple of key interactions which will perform well at a much lower overall cost.

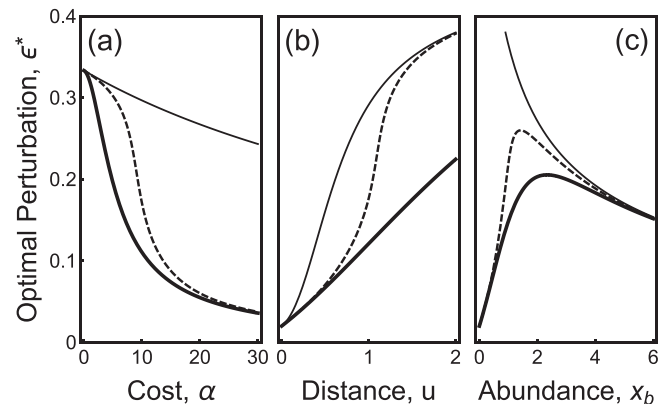


Fig. 3. Control scheme 1: Optimal perturbation to a single matrix element A_{ab} . The exact analytical solution to Eqn. (5) for the global minimum of $\mathcal{L}(\epsilon)$ (dashed) and simple asymptotic forms Eqn. (6) (thin line) and Eqn. (7) (thick line) valid for large and small values of α respectively. Parameter values are $w_a^2 = 1, x_b = 1, \vec{u} \cdot \vec{w}_a = -1, R_{ba} = -2$ and $\alpha = 10$ unless one is varied in the horizontal axes.

For this and all following numerical examples we use the parameter values and procedures described in the Methods section.

Control scheme 2: Interaction modification for minimizing community vulnerability. The interactions between species are mediated by heritable phenotypes, which, like any other trait, are selected upon. Thus, as species adapt to each other, the interaction matrix will change (Abrams and Matsuda, 1993; Abrams and Matsuda, 1997; Dieckmann and Law, 1996; Schaffer and Rosenzweig, 1978; Dercole and Rinaldi, 2008; Friesen et al., 2004; Valdovinos et al., 2010; Smith et al., 2015). In particular, it was shown experimentally that interactions typically change in one direction (Fiegna et al., 2015; Rivett et al., 2016).

In this section we address which matrix element we should modify, and by how much, $A_{ab} \rightarrow A_{ab} + \epsilon$, in order to minimize the expected equilibrium displacement upon a latter change $A_{cd} \rightarrow A_{cd} + \zeta$ on some random (c, d) .

Since we cannot know ahead of time where the random mutation may occur, we aim to minimize the displacement averaged over all possible end locations (c, d) , while also taking into account the cost of modification as before. To this end, we define a cost function,

$$\mathcal{L} = \langle |\vec{y} - \vec{x}|^2 \rangle_{cd} + \alpha \epsilon^2.$$

If we assume that the changes in the interaction matrix are small ($\epsilon R_{ba} \ll 1$ and $\zeta R_{dc} \ll 1$) then we can use the formulation present in the previous section twice. When both shifts are small, the new fixed point of the community can be linearized such that $\vec{y} \simeq \vec{x} - \epsilon x_b \vec{w}_a - \zeta x_d \vec{w}_c$. In this case,

$$\mathcal{L} \simeq \epsilon^2 x_b^2 w_a^2 + \zeta^2 x_d^2 w_c^2 + 2\epsilon \zeta x_b x_d \langle \vec{w}_a \cdot \vec{w}_c \rangle_c + \alpha \epsilon^2, \quad (12)$$

where the first term represents the displacement from the initial fixed point caused by the preventive modification, the second is the expected displacement the initial fixed point, the third represents the “preventive” benefit caused by our modification, and the final term is the cost of the modification. Setting $d\mathcal{L}/d\epsilon = 0$ we find the optimal modification if we were to implement it at (a, b)

$$\epsilon^* = -\zeta x_b \langle x \rangle \langle \vec{w}_a \cdot \vec{w}_c \rangle_c / (x_b^2 w_a^2 + \alpha), \quad (13)$$

and the optimal cost is given by

$$\mathcal{L}^* = \mathcal{L}(\epsilon^*) = \zeta^2 x^2 \langle w_c^2 \rangle_c - (x_b^2 w_a^2 + \alpha) \epsilon^{*2}. \quad (14)$$

Note that in absence of any preventive modification ($\epsilon = 0$) the cost function is just the expected average displacement from \vec{x} .

As before, Eqn. (14) is constrained between two parabolas given by substituting $x_b^2 w_a^2 \rightarrow 0$ and $x_{\max}^2 w_{\max}^2$. These two parabolas are shown in Fig. 4.

Minimizing the cost across all possible locations (a, b) is equivalent to maximizing the second term

$$\max_{ab} (x_b^2 |\vec{w}_a|^2 + \alpha) \epsilon^{*2} = \max_{ab} \frac{\zeta^2 x_b^2 \langle \vec{w}_a \cdot \vec{w}_c \rangle_c^2}{x_b^2 w_a^2 + \alpha}.$$

Fixing a gives a monotonically increasing function of x_b . Thus again, it is best to pick the b for which x_b is the largest. Then maximizing with respect to a requires

$$a = \operatorname{argmax}_a [\langle \vec{w}_a \cdot \vec{w}_c \rangle_c^2 / (x_{\max}^2 w_a^2 + \alpha)].$$

In the large α limit ($\alpha \gg x_b^2 w_{\max}^2$) the best a is the one corresponding to the w_a which on average gives the largest dot product with the average \vec{w}

$$a = \operatorname{argmax}_a \langle \vec{w}_a \cdot \vec{w}_c \rangle_c = \operatorname{argmax}_a [\langle \vec{w}_a \cdot \vec{w} \rangle].$$

In other words, we would like to pick the \vec{w} that has the largest projection onto the average \vec{w} . Applying the small α limit ($\alpha \ll x_b^2 w_{\max}^2$)

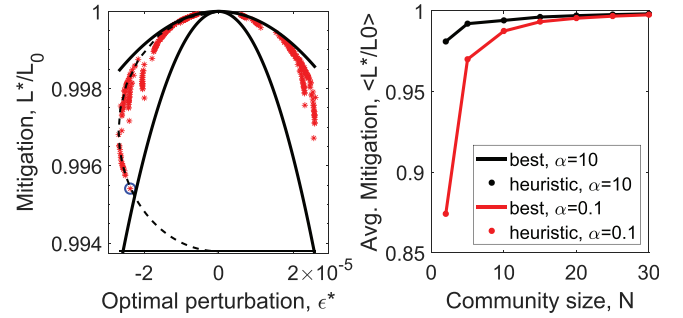


Fig. 4. Control scheme 2: Optimal preventive modifications. We plot Eqn. (13) for all (a, b) pairs (left) for $\alpha = 10$. The blue circle is the (a, b) for which $x_b = x_{\max}$ and $a = \operatorname{argmax}_a \langle \vec{w}_a \cdot \vec{w} \rangle$ and indeed minimizes \mathcal{L} . The solid black bounding lines are based on Eqn. (14) for $x_b^2 w_a^2 \rightarrow 0$ and $x_{\max}^2 w_{\max}^2$. The dashed ellipse is a sweep varying x for the “best” \vec{w}_a in Eqn. (13) and Eqn. (14) on normalized coordinates. The thin horizontal limit shows the limit as the $x \rightarrow \infty$ for the best \vec{w}_a . We compare the average performance (right) for different community sizes using our heuristic method (dots) against the best performance found by testing all possible cases (lines). For system parameters cf. Methods.

gives the same result. Sweeping across possible values for x in Eqn. (14) for some finite value of α and fixed \vec{w}_a draws an half-ellipse located on the positive or negative side depending on the sign of ϵ^* as shown by the dashed line in Fig. 4.

We generate a random interaction matrix and show with red asterisks, the improvement in \mathcal{L} upon modifying different (a, b) pairs in Fig. 4. The best (a, b) pair, chosen according to the arguments presented above, is marked blue, and indeed minimizes \mathcal{L} .

We observe that while the best position which minimizes our cost function does not necessarily provide the best reduction in displacement per ϵ , it is among the best performers. For example, in Fig. 4, left, minuscule change of $\epsilon^* = -2.4 \times 10^{-5}$ in an optimally chosen interaction matrix element ($A_{ab} = 6.6 \times 10^{-2}$) can reduce the displacement of abundances by $\sim 0.2\%$ for a 30 species community. While the ratio of these numbers are impressive, the absolute scale of change is small. Furthermore, for large communities, this very effective manipulation does not scale up to larger changes: we can improve the resilience of a large community only so much by manipulating only a single interaction. In contrast, we find that smaller communities have higher relative reductions in displacement than larger communities (cf. Fig. 4, right).

Control scheme 3: Introducing an exogenous species for displacing equilibrium. For our third control scheme we consider the possibility of choosing an exogenous species from a library of options, with given interactions and then determining how these interactions should be edited as to displace the equilibrium abundances of the community as close as possible to a given target. As before, we will account for the difficulty in making such changes and introduce a cost per change.

More specifically, we will first insert a new column \vec{a} (defining how the old species influence the new one) and new row \vec{b}^T (defining how the new species influences the old ones) into the interaction matrix. We then ask how this given \vec{a} should be edited. We do not edit \vec{b}^T , not because it is difficult experimentally or analytically, but because it is unnecessary.

After we introduce the new species, the interaction matrix \mathbf{A} and intrinsic growth rate vector \vec{r} , will turn into \mathbf{B} and \vec{s} defined by

$$\mathbf{B} = \begin{bmatrix} \mathbf{A} & \vec{a} + \vec{e} \\ \vec{b}^T & c \end{bmatrix}, \quad \vec{s} = \begin{bmatrix} \vec{r} \\ v \end{bmatrix}, \quad (15)$$

where \vec{e} is our modification to the control species and (c, v) are its self-competition and intrinsic growth. The new interaction matrix \mathbf{B} and growth rates \vec{s} characterize the new community composed to

$N + 1$ species. Using block matrix inversion and the fixed point condition we determine how the modification \vec{e} affects the equilibrium abundance of the introduced species q , and that of the original species \vec{z}

$$q = -\frac{\vec{b} \cdot \vec{x} + v}{c - \vec{b}^T \mathbf{R}(\vec{a} + \vec{e})}, \quad \vec{z} = \vec{x} - q\mathbf{R}(\vec{a} + \vec{e}). \quad (16)$$

Suppose \vec{y} is the desired target abundances for the original species. We can plug in \vec{y} for \vec{z} above and directly solve for \vec{e}^* that will get us on target

$$\vec{e}^* = c\mathbf{A}(\vec{y} - \vec{x}) / (v + \vec{b} \cdot \vec{y}) - \vec{a}. \quad (17)$$

Now we again introduce the cost of making changes to interspecies interactions. We do so by parameterizing the total modification as $\vec{e} = m\vec{e}^*$, where m takes a value between 0 (no modification) and 1 (reach target). Now that we have a cost the abundances we aim for, \vec{y} will have to be different than the abundances we get \vec{z} .

In this case, the modified equilibrium is

$$\vec{z} = \vec{x} + \frac{(v + \vec{b} \cdot \vec{x})\mathbf{R}(\vec{a} + m\vec{e}^*)}{\vec{b}^T \mathbf{R}\vec{e}^*(m_s - m)}, \quad m_s = \frac{c - \vec{b}^T \mathbf{R}\vec{a}}{\vec{b}^T \mathbf{R}\vec{e}^*}.$$

Note that as m approaches m_s we hit the singularity $|\vec{z}| \rightarrow \infty$ as before. We are interested in dialing up the modification magnitude m between 0 and 1 as to minimize the cost function

$$L = |\vec{y} - \vec{z}(m)|^2 + \alpha m^2 |\vec{e}^*|^2.$$

As before, the modification cost $\alpha m^2 |\vec{e}^*|^2$ competes against the distance cost $|\vec{y} - \vec{z}|^2$. We set the derivative to zero and solve for m^*

$$\frac{dL}{dm} \Big|_{m^*} = -2[\vec{y} - \vec{z}(m^*)] \cdot \frac{d\vec{z}}{dm} \Big|_{m^*} + 2\alpha m^* |\vec{e}^*|^2 = 0$$

$$\frac{d\vec{z}}{dm} \Big|_{m^*} = \frac{(v + \vec{b} \cdot \vec{x})\mathbf{R} \cdot \vec{a} + m_s \vec{e}^*}{\vec{b}^T \mathbf{R}\vec{e}^* (m_s - m^*)^2}.$$

This is a quartic equation in m^* of the form

$$q_0 + q_1 m^* + q_2 m^{*2} + q_3 m^{*3} + q_4 m^{*4} = 0 \quad (18)$$

which has an exact analytical solution (Weisstein, 2020), given in terms of the coefficients,

$$q_0 = 2|\mathbf{F}\vec{a}|^2 + (|\mathbf{F}\vec{e}^*|^2 + 2\vec{a}^T \mathbf{F}\vec{e}^* - 2\vec{u}^T \mathbf{F}\vec{a})m_s - 2\vec{u}^T \mathbf{F}\vec{e}^* m_s^2,$$

$$q_1 = 2\vec{a}^T \mathbf{F}\vec{e}^* + |\mathbf{F}\vec{e}^*|^2 + 2\vec{u}^T \mathbf{F}\vec{a} + 2\vec{u}^T \mathbf{F}\vec{e}^* m_s + 2\alpha |\vec{e}^*|^2 m_s^3,$$

$$q_2 = -6\alpha |\vec{e}^*|^2 m_s^2, q_3 = 6\alpha |\vec{e}^*|^2 m_s, q_4 = -2\alpha |\vec{e}^*|^2, \text{ and}$$

$$\mathbf{F} = (v + \vec{b} \cdot \vec{x})\mathbf{R} / (\vec{b}^T \mathbf{R}\vec{e}^*).$$

If the amount of modification is too small to overcome a possible increase in distance due to \vec{a} , then we must also reject this solution.

We illustrate our result in Fig. 5. First, we randomly generate a community and a control species (cf. Methods), and then applied an interaction modification to it and introduced it into the community at a time marked by the red dot. We try out two targets, constrained by some small, finite cost.

In Fig. 5, left, we introduce a new species with the intention of eradicating a ‘‘pest’’ while leaving all others unaffected. We should emphasize that the control species does not only predate on the pest, but interacts with all species to compensate for the lack of the pest in the final system. The meaning of this is that a predator that interacts solely with a single pest cannot eliminate the pest without causing a disruption to the whole system. If we want to eliminate or reduce a pest while also keeping all other species’ abundances from shifting, the controller must also modify the interactions between the control agent and other species.

In Fig. 5, right, we set another target. We introduce a new species with the intention of equalizing all abundances. Since in both

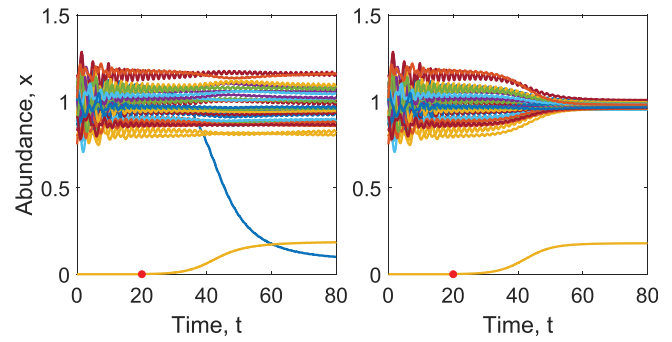


Fig. 5. Control Scheme 3: Introducing edited exogenous species. To illustrate the effectiveness of our equations we work out two examples where (left) we drive a ‘‘pest’’ towards extinction while keeping others unperturbed, and (right) we equalize all species abundances to 1. The control species is introduced at $t = 20$ (red dot, $\alpha = 10^{-3}$) by a very small amount (10^{-3}) and even after fixing, is much smaller (~ 0.1) than the others, but still able to significantly displace equilibrium. For system parameters cf. Methods.

examples there is a small but finite cost α to making modifications, we approach but do not hit our targets exactly.

In Fig. 6 we study how well communities of different sizes can be controlled as a function of cost per modification α for schemes 1 and 3. Fig. 6a (scheme 3) and Fig. 6b (scheme 1) shows the fractional reduction in distance from the desired target while Fig. 6c (scheme 3) and Fig. 6d (scheme 1) shows the total cost of applying the optimal modification.

As we see in Fig. 6, for very small α values, we end up paying little because it is cheap to make whatever change necessary to get as close as possible to our target. Interestingly, for very large α values, we end up paying little as well. In this case, the cost per change is so high that we are prohibited from making any change.

In scheme 3, viewing Fig. 6a as a step function, and Fig. 6c as a sharp spike at α_c , we can say that if the price of modifying the interactions α is cheaper than α_c , then we reach our target. Otherwise we do not. A similar statement can be made for scheme 1 (although, as mentioned before, since we are changing only a single matrix element, we cannot always exactly reach the target).

Interestingly, the critical price point α_c also happens to get us to pay the largest total cost (Fig. 6c). A hypothetical ‘‘interaction modification company’’ would be best off pricing their services at α_c per modification. If the price is far above, no one will buy their service. If far below, everyone will buy but pay nothing.

Another interesting economic observation is the non-monotonicity of the peak heights in Fig. 6c as a function of community size. Apparently our hypothetical company profits most from modifying communities that are neither too large, nor too small when trying to introduce exogenous species (scheme 3) but will profit the most when modifying single interactions (scheme 1) in small communities (Fig. 6d).

In Fig. 6a, we see that α_c is smaller for larger communities. This means that it is possible to modify larger communities only with cheap services. This is because control species introduced into large communities must have many interaction values edited.

Fine Print: Check if the optimal solution is positive, stable, and close. So far we solved for optimal perturbations to modify the composition or resilience of a community. However, there are a number of check boxes to verify before moving forward with these solutions.

First, we must check that the optimal solution is physically realizable. This solution requires an equilibrium position with non-negative species abundances with a stable trajectory from species modification (schemes 1 & 2) or introduction (scheme 3) towards the optimal equilibrium. Some target objectives may require

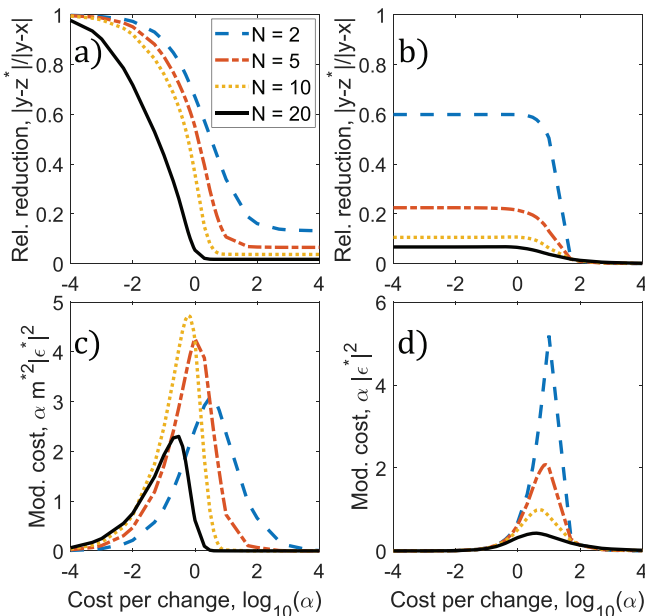


Fig. 6. Economics of species editing. We generate random communities and shift their equilibrium by using randomly generated (and then systematically edited) exogenous species (left column) or by only modifying a single interaction which gives the best result (right column). Top row: Plotting the average relative reduced distance from the desired target as a function of cost shows an abrupt transition: once the cost of interaction modification is below a critical threshold we are able to introduce the changes necessary to approach our target. Bottom row: The average total cost of species editing, $\alpha m^{-2} |\vec{\epsilon}|^2$, for the exogenous species and the single interaction, $\alpha |\epsilon|^2$. For $\alpha \rightarrow 0$, we reach our target without needing to pay much for scheme 3 but are restricted by the natural displacement directions in the community in scheme 1. For $\alpha \rightarrow \infty$ we are prohibited from making any changes, so again, do not pay much. For system parameters cf. Methods.

extinctions (i.e., pest control) which can be input into the model with zero population abundance. If there is a significant cost associated with modifications, then the optimal solution does not eradicate the target species but can severely limit their population levels. Often, this result is economically viable, and the controller is satisfied with the lower attack rates on cash crops (Zadoks, 1985).

There is an additional check box exclusive to scheme 3 via a modified biological control agent. In this case, the controller should examine the optimal solution to determine if the ecological shifts of non-targeted species are overall acceptable. For the pest eradication objective in the left plot of Fig. 5, the target objective also considered keeping non-target species abundances at pre-introduction levels. In the absence of any modifications ($\alpha \rightarrow \infty$), the population abundances post-introduction entirely depend upon the control agent's natural interactions. Historically, introductions of biological agents can have dramatic unintended consequences for the native species (Hoddle, 2004; Louda and Stiling, 2004; Messing and Wright, 2006; Schlaepfer et al., 2011; Van Driesche et al., 2010; Pearson and Callaway, 2003; Taylor, 1979; Brodeur and Rosenheim, 2000; Gerling et al., 2001; Garipey et al., 2008; Zappala et al., 2012; Hepler et al., 2020). Therefore, a balance must be reached by examining both the economic impact of the pests against the cost of control implementation and ecological disruption (Taylor, 1979; Council, 1996; Brodeur and Rosenheim, 2000; Gerling et al., 2001; Hoddle, 2004; Garipey et al., 2008; Zappala et al., 2012; Hepler et al., 2020).

4. Discussion

Theoretical limits to community control. Here we have prescribed how to modify the composition and resilience of a commu-

nity. However in doing so we also established theoretical upper limits to how much a community can be modified at best, i.e. when modification cost poses no constraint. As we see in Fig. 2 and 4, the optimal cost function \mathcal{L}^* is bound below, as shown by thin horizontal lines. For control scheme 1, this bound is

$$\mathcal{L}^* = u^2(1 - \cos^2 \theta_a).$$

For control scheme 1, we showed that hitting our target is possible only if there exist a column of \mathbf{A}^{-1} that is of the same direction as our aimed displacement \vec{u} .

In scheme 2, we showed that it is possible to increase the resilience of a community by introducing a very small perturbation to an interaction value. However as the community increases in size, even with no constraint on cost, our ability to stabilize the community becomes severely limited. The best possible performance of control scheme 2 is bounded below by

$$\mathcal{L}^* = \zeta^2 \mathbf{x}^2 \vec{w}_c^2 - \zeta^2 (\vec{w}_a \cdot \langle \vec{w} \rangle)^2 / w_a^2.$$

For control scheme 3, we prescribed how to modify exogenous species in order to shift species abundances towards a desirable target. Unlike the first two schemes, we have shown that it is possible to hit our target precisely when not constrained by cost. This relative success stems from modifying multiple interaction elements which allows us to shift the equilibrium of the system in a wide range of directions.

However, we should also caution that the solution to scheme 3 is to be rejected if it does not check a number of boxes. In our numerical tests, we have observed that if the control species is chosen without care (we randomly generate the natural interactions of the control species, as opposed to determining the “best” control species from available options such as a list of natural enemies) the probability of rejection can be rather significant. We show in the appendix the rejection rates for various reasons, for various costs and community sizes, when the natural interactions of the control species with others are randomly generated.

For practical applications, the controller can use the result given by scheme 3 to determine an ideal biological control agent. By using a non-interacting ($(\vec{a}, \vec{b}) \rightarrow 0$) control species, the interaction “modifications” returned in Eqn. (17) give the “guideline” interactions which will directly shift the equilibrium of the initial community directly to the desired target distribution. These “guidelines” can then be used to filter through a list of candidate biological control agents from which the controller can apply actual interaction modifications. Then, the controller can analyze each candidate to find the most cost-effective agent based on our framework.

What if we were allowed to modify not all of the interactions of a control species with others, but only some of them? In this case we would substitute 0 for the unchangeable components of $\vec{\epsilon}$ in Eqn. (16), and substitute our target $\vec{z} \rightarrow \vec{y}$ and hope that these overdetermined set of equations have a solution for \vec{y} . That is to say, we can shift the equilibrium exactly onto \vec{y} , only when our target vector \vec{u} can be written as a linear combination of \vec{w}_i , where i indexes the changeable components of $\vec{\epsilon}$.

Since empirically, well-controlled experiments are restrictive in scale, a researcher can use the framework presented here to evaluate the effect of connecting small-scale systems to the local or regional communities. For example, after measuring interactions between species within a greenhouse, a controller may be interested in determining the ecological effects of coupling the greenhouse community to its external environment. How do the external species interact with the smaller, well-controlled greenhouse? If the controller can modify the coupling strength by limiting exposure between external and internal greenhouse environments, how will the greenhouse's equilibrium be affected?

A researcher can address these questions by applying the single perturbation result in Eqn. 3. In this application, the coupling between internal and external environments would start at $\epsilon = 0$ (doors are closed) and can be dialed or tuned by the controller in magnitude if only certain species are allowed to interact between the two environments.

As the external-internal coupling increases in scope (i.e., more diverse interactions between external and greenhouse species), a researcher can apply the ideas used in scheme 2 in the regimes where the coupling strengths are weak. In this limit, the expected equilibrium shifts are approximately characterized by the two initially uncoupled communities. This perspective can provide an insight into the “natural” displacement vectors \bar{w}_a of the external community when the displacement vectors are well known for the internal, controlled greenhouse ecosystem. Necessarily, we have only scratched the surface of the design for such a study, but we hope that our limited analytical description can inspire research and design on how to scale up to and analyze results for larger communities.

We should be clear that our framework has many restrictions, as it hinges on well-mixedness, quasi-equilibrium, negligible demographic noise, trivial functional responses, and exclusively two-body interactions. We have also neglected any evolutionary changes that might naturally occur during the control time frame – if the interactions between species change, then the interaction parameters must be re-measured, and then our control scheme can again be used as is. The importance of evolutionary changes differs between communities depending upon species lifetime or spatial/environmental effects. For microbial systems, evolutionary changes can cause a different population dynamic behavior in as little as a few months (Lanski and Trivisano, 1994; Good et al., 2017). However, in ecosystems involving “macroorganisms” such as insect parasitoids and even larger species, the controller can ignore these evolutionary effects during the control period (Holt and Hochberg, 1997; Roderick and Navajas, 2003). Analytical studies of communities with evolving interactions would require a higher degree of complexity and vastly increases the number of parameters than the equilibrium analysis in this work (see for example, Nguyen and Vural, 2021).

Despite the limitations mentioned above, our results are transparent, analytical and illustrative, and should therefore serve as a valuable guideline for experimental, natural, agricultural and industrial systems that approximately satisfy our starting assumptions. It should serve also as a comparative benchmark and a limiting case for more complicated mathematical models of population dynamics that do not admit analytical solutions as easily.

Authors' Contributions

Vu A.T. Nguyen and Dervis Can Vural formulated and solved the problem, prepared the figures and wrote the manuscript.

Data Accessibility Statement

The MATLAB code used to simulate and generate the figures can be found at on Mendeley Data (DOI: 10.17632/n4nydr568r.1).

CRediT authorship contribution statement

Vu A.T. Nguyen: Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Investigation, Visualization, Writing - original draft, Writing - review & editing. **Dervis Can Vural:** Conceptualization, Methodology, Resources, Writing -

review & editing, Supervision, Visualization, Funding acquisition, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Abdala-Roberts, L., Agrawal, A.A., Mooney, K.A., 2012. Ant-aphid interactions on *Asclepias syriaca* are mediated by plant genotype and caterpillar damage. *Oikos* 121 (11), 1905–1913.
- Abrams, P.A., Matsuda, H., 1993. Effects of adaptive predatory and anti-predator behaviour in a two-prey-one-predator system. *Evolutionary Ecology* 7 (3), 312–326.
- Abrams, P.A., Matsuda, H., 1997. Prey adaptation as a cause of predator-prey cycles. *Evolution* 51 (6), 1742–1750.
- Abrol, D.P., Shankar, U., 2014. Pesticides, food safety and integrated pest management. In: *Integrated pest management*. Springer, pp. 167–199.
- Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A., Meiners, J.M., Tredennick, A.T., Veblen, K.E., 2018. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology letters* 21 (9), 1319–1329.
- Baek, H., 2010. Dynamic complexities of a three-species beddington-deangelis system with impulsive control strategy. *Acta Applicandae Mathematicae* 110 (1), 23–38.
- Bale, J., Van Lenteren, J., Bigler, F., 2008. Biological control and sustainable food production. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363 (1492), 761–776.
- Barker, H.L., Holeski, L.M., Lindroth, R.L., 2018. Genotypic variation in plant traits shapes herbivorous insect and ant communities on a foundation tree species. *PLoS one* 13, (7) e0200954.
- Blakney, A.K., Ip, S., Geall, A.J., 2021. An update on self-amplifying mRNA vaccine development. *Vaccines* 9 (2), 97.
- Bouskila, A., 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* 76 (1), 165–178.
- Brodeur, J., Rosenheim, J.A., 2000. Intraguild interactions in aphid parasitoids. *Entomologia experimentalis et applicata* 97 (1), 93–108.
- Broekgaarden, C., Poelman, E.H., Steenhuis, G., Voorrips, R.E., Dicke, M., Vosman, B., 2008. Responses of *Brassica oleracea* cultivars to infestation by the aphid *Brevicoryne brassicae*: an ecological and molecular approach. *Plant, Cell & Environment* 31 (11), 1592–1605.
- Carrara, F., Giometto, A., Seymour, M., Rinaldo, A., Altermatt, F., 2015. Inferring species interactions in ecological communities: a comparison of methods at different levels of complexity. *Methods in Ecology and Evolution* 6 (8), 895–906.
- Caruso, C.M., Maherali, H., Martin, R.A., 2020. A meta-analysis of natural selection on plant functional traits. *International Journal of Plant Sciences* 181 (1), 44–55.
- Carvalho, F.P., 2006. Agriculture, pesticides, food security and food safety. *Environmental science & policy* 9 (7–8), 685–692.
- Carvalho, F.P., 2017. Pesticides, environment, and food safety. *Food and Energy Security* 6 (2), 48–60.
- Chalmandrier, L., Hartig, F., Laughlin, D.C., Lischke, H., Pichler, M., Stouffer, D.B., Pellissier, L., 2021. Linking functional traits and demography to model species-rich communities. *Nature Communications* 12 (1), 1–9.
- Cheng, H., Wang, F., and Zhang, T. (2012). Multi-state dependent impulsive control for holling i predator-prey model. *Discrete Dynamics in Nature and Society*, 2012..
- Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31 (1), 343–366.
- Council, N.R. et al., 1996. Ecologically based pest management: new solutions for a new century. National Academies Press.
- De Leenheer, P., Smith, H., 2003. Feedback control for chemostat models. *Journal of Mathematical Biology* 46 (1), 48–70.
- Dercole, F., Rinaldi, S., 2008. Analysis of evolutionary processes: the adaptive dynamics approach and its applications, volume 3. Princeton University Press.
- Dieckmann, U., Law, R., 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34 (5–6), 579–612.
- Dormann, C.F., 2007. Competition hierarchy, transitivity and additivity: investigating the effect of fertilisation on plant-plant interactions using three common bryophytes. *Plant Ecology* 191 (2), 171–184.
- Englund, G., Öhlund, G., Hein, C.L., Diehl, S., 2011. Temperature dependence of the functional response. *Ecology letters* 14 (9), 914–921.

- Fernández, F.J., Garay, J., Móri, T.F., Csiszár, V., Varga, Z., López, I., Gámez, M., Cabello, T., 2021. Theoretical foundation of the control of pollination by hoverflies in a greenhouse. *Agronomy* 11 (1), 167.
- Fiegna, F., Moreno-Letelier, A., Bell, T., Barraclough, T.G., 2015. Evolution of species interactions determines microbial community productivity in new environments. *ISME J* 9 (5), 1235–1245.
- Friesen, M.L., Saxer, G., Travisano, M., Doebeli, M., 2004. Experimental evidence for sympatric ecological diversification due to frequency-dependent competition in *Escherichia coli*. *Evolution* 58 (2), 245–260.
- Friman, V.-P., Jousset, A., Buckling, A., 2014. Rapid prey evolution can alter the structure of predator–prey communities. *Journal of Evolutionary Biology* 27 (2), 374–380.
- Garipey, T., Kuhlmann, U., Gillott, C., Erlandson, M., 2008. A large-scale comparison of conventional and molecular methods for the evaluation of host–parasitoid associations in non-target risk-assessment studies. *Journal of Applied Ecology* 45 (2), 708–715.
- Georgescu, P. (2011). On the impulsive control of a n-prey and one-predator food web model. In *Proceedings of The International Conference on Applied and Pure Mathematics, Iasi, Romania, Bull. Inst. Pol. Iasi, volume 57, pages 111–123.*
- Gerling, D., Alomar, Ò., Arnò, J., 2001. Biological control of *Bemisia tabaci* using predators and parasitoids. *Crop Protection* 20 (9), 779–799.
- Girard, P., Meissner, P., Jordan, M., Tsao, M., Wurm, F., 1999. Small scale bioreactor system for process development and optimization. In: *Animal Cell Technology: Products from Cells, Cells as Products*. Springer, pp. 323–327.
- Good, B.H., McDonald, M.J., Barrick, J.E., Lenski, R.E., Desai, M.M., 2017. The dynamics of molecular evolution over 60,000 generations. *Nature* 551 (7678), 45–50.
- Griffiths, J.L., Warren, P.H., Childs, D.Z., 2015. Multiple environmental changes interact to modify species dynamics and invasion rates. *Oikos* 124 (4), 458–468.
- Hays, W.S., Conant, S., 2007. Biology and impacts of Pacific island invasive species. 1. a worldwide review of effects of the small Indian mongoose, *Herpestes javanicus* (Carnivora: Herpestidae). *Pacific Science* 61 (1), 3–16.
- Hepler, J.R., Athey, K., Enicks, D., Abram, P.K., Garipey, T.D., Talamas, E.J., Beers, E., 2020. Hidden host mortality from an introduced parasitoid: Conventional and molecular evaluation of non-target risk. *Insects* 11 (11), 822.
- Hoddle, M.S., 2004. Restoring balance: using exotic species to control invasive exotic species. *Conservation Biology* 18 (1), 38–49.
- Holt, R.D., Hochberg, M.E., 1997. When is biological control evolutionarily stable (or is it)? *Ecology* 78 (6), 1673–1683.
- Jiang, G., Lu, Q., 2007. Impulsive state feedback control of a predator–prey model. *Journal of Computational and Applied Mathematics* 200 (1), 193–207.
- Jiang, G., Lu, Q., Qian, L., 2007. Complex dynamics of a holling type II prey–predator system with state feedback control. *Chaos, Solitons & Fractals* 31 (2), 448–461.
- Jones-Baumgardt, C., Llewellyn, D., Zheng, Y., 2020. Different microgreen genotypes have unique growth and yield responses to intensity of supplemental PAR from light-emitting diodes during winter greenhouse production in southern Ontario, Canada. *HortScience* 55 (2), 156–163.
- Lamit, L.J., Busby, P.E., Lau, M.K., Simpson, Z.G., Wojtowicz, T., Keith, A.R., Zinkgraf, M.S., Schweitzer, J.A., Shuster, S.M., Gehring, C.A., et al., 2015. Tree genotype mediates covariance among communities from microbes to lichens and arthropods. *Journal of Ecology* 103 (4), 840–850.
- Lemoine, N.P., Hoffman, A., Felton, A.J., Baur, L., Chaves, F., Gray, J., Yu, Q., Smith, M. D., 2016. Underappreciated problems of low replication in ecological field studies. *Ecology* 97 (10), 2554–2561.
- Lenski, R.E., Travisano, M., 1994. Dynamics of adaptation and diversification: a 10,000-generation experiment with bacterial populations. *Proceedings of the National Academy of Sciences* 91 (15), 6808–6814.
- Liu, X., Chen, L., 2003. Complex dynamics of holling type II lotka–volterra predator–prey system with impulsive perturbations on the predator. *Chaos, Solitons & Fractals* 16 (2), 311–320.
- Liu, B., Teng, Z., Chen, L., 2006. Analysis of a predator–prey model with holling II functional response concerning impulsive control strategy. *Journal of Computational and Applied Mathematics* 193 (1), 347–362.
- Louda, S.M., O'Brien, C.W., 2002. Unexpected ecological effects of distributing the exotic weevil, *Larinus planus* (f.), for the biological control of Canada thistle. *Conservation Biology* 16 (3), 717–727.
- Louda, S.M., Stiling, P., 2004. The double-edged sword of biological control in conservation and restoration. *Conservation Biology* 18 (1), 50–53.
- MacArthur, R., 1969. Species packing, and what competition minimizes. *Proceedings of the National Academy of Sciences* 64 (4), 1369–1371.
- Margiotta, M., Bella, S., Buffa, F., Caleca, V., Floris, I., Giorno, V., Lo Verde, G., Rapisarda, C., Sasso, R., Suma, P., et al., 2017. Modeling environmental influences in the psyllaephagus *bliteus* (Hymenoptera: Encyrtidae)–glycaspis *brimblecombei* (Hemiptera: Aphalaridae) parasitoid–host system. *Journal of Economic Entomology* 110 (2), 491–501.
- Mazenc, F., Jiang, Z.-P., 2009. In: Time-varying control laws with guaranteed persistence for a class of multi-species chemostats. In *Proceedings of the 48th IEEE Conference on Decision and Control (CDC) held jointly with 2009 28th Chinese Control Conference*. IEEE, pp. 7710–7715.
- Mazenc, F., Malisoff, M., 2012. Stability and stabilization for models of chemostats with multiple limiting substrates. *Journal of Biological Dynamics* 6 (2), 612–627.
- Messing, R.H., Wright, M.G., 2006. Biological control of invasive species: solution or pollution? *Frontiers in Ecology and the Environment* 4 (3), 132–140.
- Mooney, K.A., 2011. Genetically based population variation in aphid association with ants and predators. *Arthropod-Plant Interactions* 5 (1), 1–7.
- Mooney, K.A., Agrawal, A.A., 2008. Plant genotype shapes ant-aphid interactions: implications for community structure and indirect plant defense. *The American Naturalist* 171 (6), E195–E205.
- Mugabo, M., Gilljam, D., Petteway, L., Yuan, C., Fowler, M.S., Sait, S.M., 2019. Environmental degradation amplifies species' responses to temperature variation in a trophic interaction. *Journal of Animal Ecology* 88 (11), 1657–1669.
- Mühlbauer, L.K., Schulze, M., Harpole, W.S., Clark, A.T., 2020. gausser: Simple methods for fitting lotka–volterra models describing gause's "struggle for existence". *Ecology and Evolution* 10 (23), 13275–13283.
- Nguyen, V.A., Can Vural, D., 2021. Extinction in complex communities as driven by adaptive dynamics. *Journal of Evolutionary Biology*.
- Niehaus, L., Boland, I., Liu, M., Chen, K., Fu, D., Henckel, C., Chaung, K., Miranda, S.E., Dyckman, S., Crum, M., Dedrick, S., Shou, W., Momeni, B., 2019. Microbial coexistence through chemical-mediated interactions. *Nature Communications* 10 (1), 1–12.
- Nonomura, T., Toyoda, H., 2020. Soil surface-trapping of tomato leaf-miner flies emerging from underground pupae with a simple electrostatic cover of seedbeds in a greenhouse. *Insects* 11 (12), 878.
- O'Dwyer, J.P., 2018. Whence lotka–volterra? *Theoretical Ecology* 11 (4), 441–452.
- Paulitz, T.C., Bélanger, R.R., 2001. Biological control in greenhouse systems. *Annual Review of Phytopathology* 39 (1), 103–133.
- Pearson, D.E., Callaway, R.M., 2003. Indirect effects of host-specific biological control agents. *Trends in Ecology & Evolution* 18 (9), 456–461.
- Pei, Y., Chen, L., Zhang, Q., Li, C., 2005. Extinction and permanence of one-prey multi-predators of holling type II functional response system with impulsive biological control. *Journal of Theoretical Biology* 235 (4), 495–503.
- Rafikov, M., Balthazar, J.M., Von Bremen, H., 2008. Mathematical modeling and control of population systems: applications in biological pest control. *Applied Mathematics and Computation* 200 (2), 557–573.
- Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., Petchey, O.L., 2012. Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367 (1605), 2923–2934.
- Ratzke, C., Gore, J., 2018. Modifying and reacting to the environmental pH can drive bacterial interactions. *PLoS Biology* 16 (3), e2004248.
- Rivett, D.W., Scheuerl, T., Culbert, C.T., Mombrikotb, S.B., Johnstone, E., Barraclough, T.G., Bell, T., 2016. Resource-dependent attenuation of species interactions during bacterial succession. *ISME J* 10 (9), 2259–2268.
- Roderick, G.K., Navajas, M., 2003. Genes in new environments: genetics and evolution in biological control. *Nature Reviews Genetics* 4 (11), 889–899.
- Rosic, N., Bradbury, J., Lee, M., Baltrotsky, K., Grace, S., 2020. The impact of pesticides on local waterways: A scoping review and method for identifying pesticides in local usage. *Environmental Science & Policy* 106, 12–21.
- Royauté, R., Pruitt, J.N., 2015. Varying predator personalities generates contrasting prey communities in an agroecosystem. *Ecology* 96 (11), 2902–2911.
- Schaffer, W.M., Rosenzweig, M.L., 1978. Homage to the red queen. I. coevolution of predators and their victims. *Theoretical Population Biology* 14 (1), 135–157.
- Schlaepfer, M.A., Sax, D.F., Olden, J.D., 2011. The potential conservation value of non-native species. *Conservation Biology* 25 (3), 428–437.
- Sentis, A., Hemptinne, J.-L., Brodeur, J., 2012. Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency. *Oecologia* 169 (4), 1117–1125.
- Shanmuganathan, T., Pallister, J., Doody, S., McCallum, H., Robinson, T., Sheppard, A., Hardy, C., Halliday, D., Venables, D., Voysey, R., et al., 2010. Biological control of the cane toad in Australia: a review. *Animal Conservation* 13, 16–23.
- Sih, A., Crowley, P., McPeck, M., Petranka, J., Strohmeier, K., 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16 (1), 269–311.
- Singh, B.K., Dawson, L.A., Macdonald, C.A., Buckland, S.M., 2009. Impact of biotic and abiotic interaction on soil microbial communities and functions: A field study. *Applied Soil Ecology* 41 (3), 239–248.
- Smith, D.S., Lau, M.K., Jacobs, R., Monroy, J.A., Shuster, S.M., Whitham, T.G., 2015. Rapid plant evolution in the presence of an introduced species alters community composition. *Oecologia* 179 (2), 563–572.
- Snyder, G.B., Finke, D.L., Snyder, W.E., 2008. Predator biodiversity strengthens aphid suppression across single- and multiple-species prey communities. *Biological Control* 44 (1), 52–60.
- Sommer, U., 1983. Nutrient competition between phytoplankton species in multispecies chemostat experiments. *Archiv für Hydrobiologie* 96, 399–416.
- Sun, K., Kasperski, A., Tian, Y., Chen, L., 2011. Modelling and optimization of a continuous stirred tank reactor with feedback control and pulse feeding. *Chemical Engineering and Processing: Process Intensification* 50 (7), 675–686.
- Talebi, K., Hosseininaveh, V., and Ghadayari, M. (2011). Ecological impacts of pesticides in agricultural ecosystem. *Pesticides in the Modern World-Risks and Benefits* (M. Stoytcheva, ed.). In *Tech Open Access Publisher, Rijeka, Croatia, pages 143–168.*
- Tang, Y., Ma, X., Li, M., Wang, Y., 2020. The effect of temperature and light on strawberry production in a solar greenhouse. *Solar Energy* 195, 318–328.
- Taylor, J., 1979. *Sensoriaphis* in western Australia. *Bulletin of the Royal Entomological Society of London* 3.
- Télez, M., Cabello, T., Gámez, M., Burguillo, F., Rodríguez, E., 2020. Comparative study of two predatory mites *Amblyseius swirskii* athias-henriot and *traneius montdorensis* (schicha) by predator–prey models for improving biological control of greenhouse cucumber. *Ecological Modelling* 431, 109197.

- Tétard-Jones, C., Kertész, M.A., Gallois, P., Preziosi, R.F., 2007. Genotype-by-genotype interactions modified by a third species in a plant-insect system. *The American Naturalist* 170 (3), 492–499.
- Tonnang, H.E., Nedorezov, L.V., Ochanda, H., Owino, J., Löhr, B., 2009. Assessing the impact of biological control of *plutella xylostella* through the application of lotka–volterra model. *Ecological Modelling* 220 (1), 60–70.
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecology letters* 11 (12), 1351–1363.
- Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P., Dunne, J.A., 2010. Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology letters* 13 (12), 1546–1559.
- Van Driesche, R., Carruthers, R., Center, T., Hoddle, M., Hough-Goldstein, J., Morin, L., Smith, L., Wagner, D., Blossey, B., Brancatini, V., et al., 2010. Classical biological control for the protection of natural ecosystems. *Biological control* 54, S2–S33.
- Van Lenteren, J., 1983. The potential of entomophagous parasites for pest control. *Agriculture, ecosystems & environment* 10 (2), 143–158.
- Waage, J., Hassell, M., 1982. Parasitoids as biological control agents—a fundamental approach. *Parasitology* 84 (4), 241–268.
- Wei, C., Zhang, S., and Chen, L. (2013). Impulsive state feedback control of cheese whey fermentation for single-cell protein production. *Journal of Applied Mathematics*, 2013.
- Weisstein, E.W. (2020 (accessed July 7, 2020)). Quartic Equation..
- Whitham, T.G., Gehring, C.A., Lamit, L.J., Wojtowicz, T., Evans, L.M., Keith, A.R., Smith, D.S., 2012. Community specificity: life and afterlife effects of genes. *Trends in plant science* 17 (5), 271–281.
- Xu, C., Yuan, S., 2016. Competition in the chemostat: a stochastic multi-species model and its asymptotic behavior. *Mathematical biosciences* 280, 1–9.
- Yang, J., Tang, G., 2019. Piecewise chemostat model with control strategy. *Mathematics and Computers in Simulation* 156, 126–142.
- Zadoks, J., 1985. On the conceptual basis of crop loss assessment: the threshold theory. *Annual Review of Phytopathology* 23 (1), 455–473.
- Zappala, L., Bernardo, U., Biondi, A., Cocco, A., Deliperi, S., Delrio, G., Giorgini, M., Pedata, P., Rapisarda, C., Garzia, G.T., et al., 2012. Recruitment of native parasitoids by the exotic pest *tuta absoluta* in southern italy. *Bulletin of Insectology* 65 (1), 51–61.
- Zhang, Y., Yan, X., Liao, B., Zhang, Y., Ding, Y., 2016. Z-type control of populations for lotka–volterra model with exponential convergence. *Mathematical biosciences* 272, 15–23.
- Zytynska, S.E., Guenay, Y., Sturm, S., Clancy, M.V., Senft, M., Schnitzler, J.-P., Dilip Pophaly, S., Wurmser, C., Weisser, W.W., 2019. Effect of plant chemical variation and mutualistic ants on the local population genetic structure of an aphid herbivore. *Journal of Animal Ecology* 88 (7), 1089–1099.