Destabilizing evolutionary and eco-evolutionary feedbacks drive empirical eco-evolutionary cycles

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ABSTRACT: A fundamental problem in community ecology is understanding how ecological and evolutionary processes and their interactions influence system stability. We develop a method to identify how the interactions between ecological processes (ecological feedbacks), between evolutionary processes (evolutionary feedbacks), and between ecological and evolutionary processes (eco-evolutionary feedbacks) affect system stability. We apply our method to nine empirically-parameterized eco-evolutionary models of exploiter-victim systems from the literature and identify which particular feedbacks cause some systems to converge to a steady state, while others exhibit sustained oscillations. We find that ecological feedbacks involving the interactions between all species and the evolutionary and eco-evolutionary feedbacks defined by just the interactions between exploiter species (predators or pathogens) are typically stabilizing. In contrast, evolutionary and eco-evolutionary feedbacks defined by the interactions between victim species (prey or hosts) are destabilizing more often than not. When comparing stable and cyclic systems, we find that the evolutionary feedbacks are destabilizing in all cyclic systems, implying that disruptive selection is one mechanism driving the eco-evolutionary cycles. Moreover, our analysis shows that the feedbacks between ecological and evolutionary processes rarely alter the stability of the system, i.e., in nearly all cases stability of the whole system can be predicted from just the (de)stabilizing effects of the ecological and evolutionary feedbacks. We also explore how the (de)stabilizing effects of different feedbacks and the speed of evolution interact to determine the stability of the whole system. As the number of empirical studies demonstrating eco-evolutionary feedbacks increases, we can continue to apply these methods to determine whether the patterns we observe are common in other empirical communities.

Introduction

Understanding the factors that influence stability remains a fundamental problem in community ecology. Empirical and theoretical studies have demonstrated that the feedbacks between ecological and evolutionary processes, called eco-evolutionary feedbacks, can alter community stability (1; 2; 3; 4; 5; 6; 7; 8). In particular, some experimental systems with demonstrated eco-evolutionary feedbacks between population densities and evolving species traits converge to a steady state (9; 10), while others exhibit cyclic dynamics (11; 12; 3; 13; 14).

Generally, it is not well understood which particular feedbacks between population densities (ecological feedbacks), between evolving traits (evolutionary feedbacks), and between densities and traits (eco-evolutionary feedbacks) are responsible for driving stable versus cyclic population dynamics in empirical systems. Previous theoretical work (8; 15; 16; 17) has shown that ecological, evolutionary and eco-evolutionary feedbacks have the potential to be stabilizing or destabilizing, and that the strength of those effects depends on whether ecological rates of change are faster than evolutionary rates of change, or vice versa. However, we still do not know how these theoretical predictions play out in empirical systems. This disconnect is due, in part, to the fact that most of the theoretical results assume ecological rates of change are either much faster or much slower than rates of evolutionary change. In contrast, the observed ecological and evolutionary dynamics in the empirical systems cited above suggest that ecological and evolutionary change can occur at similar rates.

Additionally, many empirical systems involve multiple interacting species and multiple evolving traits. Using a predator-prey system with two species and two traits, Cortez (16) showed how to determine whether each ecological, evolutionary, and eco-evolutionary feedback has a stabilizing or destabilizing effect on the stability of whole system. However, for larger systems, this approach leads to an intractably large number of feedbacks to analyze. Moreover, unless two systems are identical in their composition of types of species and traits, how to compare feedbacks between systems is unclear. Thus, we need new theoretical tools that identify broadly the effects of ecological feedbacks, evolutionary feedbacks, and

eco-evolutionary feedbacks while simultaneously pinpointing the importance of particular feedbacks.

In this study, we develop a method that determines how the stability of the whole system is influenced by ecological, evolutionary and eco-evolutionary feedbacks and enables us to pinpoint the collective and particular effects ecological, evolutionary and eco-evolutionary feedbacks have on stability. Our method uses feedbacks defined in terms of the stabilities of complementary pairs of subsystems (e.g., ecological vs. evolutionary subsystems) and the interactions between subsystems (e.g., the effects the evolutionary subsystem has on the ecological subsystem). Here, a subsystem defines the interactions and dynamics of a set of variables when all other variables are held fixed (e.g., the ecological subsystem defines the interactions and dynamics of all population densities when all population-level traits are held fixed). We apply the method to nine models from the literature that are parameterized to empirical systems. We find that the ecological feedbacks involving the ecological dynamics of all species and the evolutionary and eco-evolutionary feedbacks defined by the dynamics of exploiters (predators or pathogens) are generally stabilizing. In contrast, evolutionary and eco-evolutionary feedbacks defined by the dynamics of victim species (prey or hosts) can be stabilizing or destabilizing. Our results suggest that eco-evolutionary feedbacks rarely alter what one would predict about system stability from just ecological and evolutionary feedbacks. We also explore how the speed of evolution and subsystem stability interact to determine the stability of the whole system. We find for half of the systems that eco-evolutionary feedbacks can alter the stability of the whole system for some range of evolutionary speeds. For the other half, we find that the eco-evolutionary feedbacks are insufficiently strong to alter the stability of the whole system for any speed of evolution.

Models, Subsystems, and Stability

Selecting parameterized eco-evolutionary models from published studies

To identify studies with parameterized eco-evolutionary models, we searched Web of Science and Google Scholar with keywords such as "eco-evolutionary dynamics" and "evolution & population dynamics". Studies were selected only if they included models that were parameterized using empirical data and that described ecological and evolutionary dynamics. Here, ecological dynamics mean changes in population densities. Evolutionary dynamics mean either changes in a continuous trait (e.g., pathogen virulence) or the frequencies of different clonal types (e.g., defended and undefended clones). Three studies (18; 19; 20) were excluded because the models did not have coexistence equilibria where there was standing genetic variation in at least one population. In total, we identified 9 studies consisting of six predator-prey models, one intraguild predation model, and two host-pathogen models; see Table 1 for a summary and appendix S1 for additional details. Multiple entries are listed in Table 1 for models with more than one parameterization; Bolker et al. (21) is the only exception because the results are identical for all four parameterizations. These nine studies represent all published studies known to the authors.

A general eco-evolutionary model

We use a general eco-evolutionary community model that encompasses the nine parameterized models from the literature. The model describes the changes in the densities of n species $(N_1, ..., N_n)$ and m population-level traits $(x_1, ..., x_m)$, e.g., mean trait values or frequencies of particular genotypes. It has been used previously to study system stability and permanence (15; 22). The model is

$$\frac{dN_i}{dt} = N_i f_i(N_1, ..., N_n, x_1, ..., x_m), \quad 1 \leq i \leq n \tag{1}$$

$$\frac{dx_j}{dt} = g_j(N_1, ..., N_n, x_1, ..., x_m), \quad 1 \leq j \leq m. \tag{2}$$

Here, f_i is the per capita fitness of species i; it accounts for all ecological interactions between species i and the other species in the community. Importantly, those interactions depend on the species traits. The functions g_j define the evolutionary dynamics for each trait, which in general are density and frequency dependent.

All of the nine parameterized models from the literature can be converted into the general form, which facilitates comparisons across systems. For example, clonal models with two clonal types (C_1, C_2) can be converted into continuous trait models by deriving equations for the total density $(N_1 = C_1 + C_2)$ and the frequency of clone 1 $(x_1 = C_1/N_1)$. Similar transformations apply for systems with more than two clonal types; see appendix S2 for details. In addition, the general model is flexible enough to account for common intraspecific and interspecific species interactions (e.g., cooperation, competition, predation, and mutualism). It is also flexible enough to encompass other bodies of eco-evolutionary theory based on adaptive dynamics (23; 24) and quantitative genetics (25).

The stability of model (1) is defined by whether the system converges to a coexistence equilibrium (hereafter a stable system) or the coexistence equilibrium is unstable and the system exhibits cyclic dynamics (hereafter an unstable system). The stability of an equilibrium is determined by the Jacobian (J), i.e., a derivative matrix that determines whether small perturbations from equilibrium decay (implying stability) or grow (implying instability). Mathematically, an equilibrium is stable if all eigenvalues of the Jacobian have negative real parts and it is unstable if any eigenvalue has positive real part.

Complimentary subsystem pairs and subsystem stability

Our method focuses on the stabilities of complementary pairs of subsystems. A subsystem describes the dynamics of a subset of variables when all other variables are fixed at their equilibrium values. Two subsystems form a complementary pair if together the subsystems include all variables in the system without overlap (i.e., the subsystems contain disjoint sets of variables whose union is all variables in the system). For example, the (n-dimensional) ecological subsystem describes the population dynamics of all species (dN_i/dt equations) when all traits are fixed at their equilibrium values (solid box in figure 1B). Its complement is the (m-dimensional) evolutionary subsystem (dashed box in figure 1B), which describes the evolutionary dynamics of all traits (dx_j/dt equations) when all population densities are fixed at their equilibrium values. Alternatively, an eco-evolutionary subsystem (solid box in figure 1C) could be the population and trait dynamics associated with one species, say N_1 and x_1. Its complementary subsystem (dashed box in figure 1C) is the population and trait dynamics of the remaining species: $N_2, \ldots, N_n, x_2, \ldots, x_m$.

The stability of a subsystem is determined by the submatrix of the Jacobian that only involves the variables in that subsystem. For example, consider an eco-evolutionary nutrient-prey-predator model where the ecological variables (N_1, N_2, N_3) are the nutrient, prey, and predator densities and the evolutionary variable is the mean prey trait (x_1); this system is illustrated in figure 1. The Jacobian for this system has the form

$$
\begin{array}{cc}
 & \begin{array}{cc} \text{Ecological Subsystem} & \text{Effects of Evo on Eco} \end{array} \\
J = & \left[\begin{array}{cc}
\begin{array}{ccc}
\frac{\partial}{\partial N_1}\frac{dN_1}{dt} & \frac{\partial}{\partial N_2}\frac{dN_1}{dt} & \frac{\partial}{\partial N_3}\frac{dN_1}{dt} \\
\frac{\partial}{\partial N_1}\frac{dN_2}{dt} & \frac{\partial}{\partial N_2}\frac{dN_2}{dt} & \frac{\partial}{\partial N_3}\frac{dN_2}{dt} \\
\frac{\partial}{\partial N_1}\frac{dN_3}{dt} & \frac{\partial}{\partial N_2}\frac{dN_3}{dt} & \frac{\partial}{\partial N_3}\frac{dN_2}{dt}
\end{array} &
\begin{array}{c}
\frac{\partial}{\partial x_1}\frac{dN_1}{dt} \\
\frac{\partial}{\partial x_1}\frac{dN_2}{dt} \\
\frac{\partial}{\partial x_1}\frac{dN_3}{dt}
\end{array} \\
\begin{array}{ccc}
\frac{\partial}{\partial N_1}\frac{dx_1}{dt} & \frac{\partial}{\partial N_2}\frac{dx_1}{dt} & \frac{\partial}{\partial N_3}\frac{dx_1}{dt}
\end{array} &
\begin{array}{c}
\frac{\partial}{\partial x_1}\frac{dx_1}{dt}
\end{array}
\end{array} \right] \\
 & \begin{array}{cc} \text{Effects of Eco on Evo} & \text{Evolutionary Subsystem} \end{array}
\end{array}
\tag{3}
$$

The top left box of the Jacobian determines the stability of the ecological subsystem (solid box in figure 1B), the bottom right box of the Jacobian determines the stability of the evolutionary subsystem (dashed box in figure 1B), and the off-diagonal boxes determine the effects of ecology on evolution (bottom left box) and the effects of evolution on ecology (top right box). The stability of the eco-evolutionary subsystem in figure 1C (solid box) is defined by the 2x2 submatrix made up of the Jacobian entries that are in the second and fourth rows and columns. Mathematically, a subsystem is unstable if its submatrix has at least one eigenvalue with positive real part; a subsystem is stable if its submatrix has all eigenvalues with negative real parts; a subsystem is neutrally stable if its submatrix has all eigenvalues with non-positive real parts and at least one eigenvalue with strictly negative real part; and a subsystem is neutral if its submatrix has all eigenvalues with zero real parts.

When there are no feedbacks between a pair of complementary subsystems, the stability of the whole system is determined by the stabilities of the subsystems. In particular, the whole system is stable if both subsystems are stable and the whole system is unstable if either subsystem is unstable. This means that stable subsystems have stabilizing effects on the stability of the whole system and unstable subsystems have destabilizing effects on the stability of the whole system. In our example above, the absence of feedbacks between the ecological and evolutionary subsystems means that all entries in either the top right box or the bottom left box are zeros. In this case, the stability of the whole system (determined by the full Jacobian) is completely determined by the stabilities of the submatrices for the ecological and evolutionary subsystems (top left and bottom right boxes).

When there are feedbacks between a pair of complementary subsystems, each subsystem still has a stabilizing or destabilizing effect on the stability of whole system, but the feedbacks between the subsystems can alter the stability predicted by the complementary pair. For example, if the ecological subsystem is stable and the evolutionary subsystem is unstable in our example from above, then the whole system is predicted to be stable in the absence of eco-evolutionary feedbacks (zero entries in the top right or bottom left boxes). However,

when eco-evolutionary feedbacks are present (non-zero entries in the top right and bottom left boxes) and those feedbacks are stabilizing, the whole system can become stable. In this case, the feedbacks between the subsystems counteract the destabilizing effects of the evolutionary subsystem and stabilize the whole system.

Complimentary subsystem pairs method

Our method uses the stabilities of complementary pairs of subsystems to predict how ecological, evolutionary, and eco-evolutionary feedbacks affect the stability of the whole system in two ways. To begin, we use the stabilities of the complementary pairs of subsystems to identify whether different subsystems have stabilizing or destabilizing effects on the whole system. Specifically, unstable subsystems have a destabilizing effect on the stability of the whole system, stable or neutrally stable subsystems have a stabilizing effect on the stability of the whole system, and neutral subsystems have no direct effect on the stability of the whole system (but can indirectly affect stability through their interactions with other subsystems). See the appendix S1 for mathematical details and justifications.

We also we compare the stabilities of the complementary subsystem pairs with the stability of the whole system in order to determine whether the feedbacks between subsystems do or do not alter system stability. There are four possibilities; the first and second correspond to cases where the feedbacks between complementary subsystems are sufficiently strong to alter system stability from what would be predicted from just the stabilities of the complementary subsystems. First, if both subsystems are stable but the whole system is unstable, then the feedbacks are destabilizing as they are sufficiently strong to counteract the stabilizing effects of the subsystems. For example, if the whole system is unstable and the n-dimensional ecological and m-dimensional evolutionary subsystems are stable, then instability of the whole system is due to destabilizing eco-evolutionary feedbacks being stronger than the stabilizing ecological and evolutionary feedbacks. Second, if one or both subsystems are unstable but the whole system is stable, then the feedbacks between the subsystems are

stabilizing as they are sufficiently strong to counteract the destabilizing effects of the unstable subsystems. For example, if the ecological subsystem is stable and the evolutionary subsystem is unstable but the whole system is stable, then stability of the whole system is caused by stabilizing ecological and eco-evolutionary feedbacks being stronger than the destabilizing evolutionary feedbacks. Third, if both subsystems are stable and the whole system is stable, then the feedbacks between the subsystems do not alter the stability of the system. In this case, the feedbacks between the subsystems are either stabilizing or destabilizing but insufficiently strong to counteract the stabilizing effects of the subsystems. Fourth, if one or both subsystems are unstable and the whole system is unstable, then the feedbacks between the subsystems do not alter the stability of the system. In this case, the feedbacks between the subsystems are either destabilizing or stabilizing but insufficiently strong to counteract the destabilizing effects of the subsystems.

When analyzing the parameterized models from the literature, we consider four pairs of complementary systems, chosen for their biological relevance. First, we use the complementary ecological and evolutionary subsystems (figure 1B) to identify broadly how ecological, evolutionary, and eco-evolutionary feedbacks involving all species influence system stability. Second, we use the evolutionary subsystem for a single species (i.e, the subsystem composed of all evolving traits of one species) and its complement (also figure 1B) to identify how the evolutionary feedbacks of a single species influence system stability. Third, we use the eco-evolutionary subsystem for a single species (i.e., the subsystem composed of the density and all evolving traits for that species) and its complement (figure 1C) to identify how the feedbacks within a single species influence system stability. Fourth, we use the subsystem defined by all species and traits in a particular trophic level and its complement (figure 1D) to identify how the feedbacks within a particular trophic level influence system stability.

Effects of varied evolutionary speed

Current theory (8; 26; 15; 16) predicts that system stability depends on both the stabilities of subsystems and the relative speeds of ecological and evolutionary change. For the particular cases where rates of evolution are much slower or much faster than rates of ecological change, stability of the whole system is determined, in part, by the stability of either the evolutionary subsystem or ecological subsystem. Specifically, stability of the whole system in the slow evolution limit is determined by the stability of the ecological subsystem and feedbacks between the ecological and evolutionary subsystems. In contrast, stability of the whole system in the fast evolution limit is determined by the stability of the evolutionary subsystem and the feedbacks between the ecological and evolutionary subsystems.

To explore how the interactions between subsystem stability and the speed of evolution influence the stability of whole system, we varied the speed of evolution in the nine parameterized models. This was done by introducing multiplicative parameters into the right hand sides of the trait equations in model (1); see appendix S2 for details. We then assessed how speeding up and slowing down the rates of evolution influenced system stability and whether system stability could be accurately predicted from just the stabilities of the ecological and evolutionary subsystems.

Results

Effects of ecological, evolutionary and eco-evolutionary feedbacks on the stabilities of empirical systems

We first explored whether different kinds of subsystems have different effects on the stability of the whole system. Our analysis of the nine parameterized models from the literature revealed that subsystem stability differed depending on subsystem type (ecological, evolutionary, or eco-evolutionary) and species trophic level (exploiter vs. victim); see Table 1.

Specifically, ecological subsystems were stable (or neutrally stable) in eight of the systems whereas evolutionary subsystems were stable in only four of the systems. Exploiter ecological, evolutionary, and eco-evolutionary subsystems were stable or neutral in seven of the nine systems. In contrast, victim ecological, evolutionary, and eco-evolutionary subsystems were stable in four of the nine systems. Taken together, this suggests that in these nine empirical systems, ecological feedbacks involving the dynamics of all species were typically stabilizing; ecological, evolutionary, and eco-evolutionary feedbacks involving the dynamics of exploiter species were typically stabilizing or neutral; and the ecological, evolutionary, and eco-evolutionary feedbacks involving the dynamics of victim species were either stabilizing or destabilizing.

We next explored whether the feedbacks between subsystems altered the stability of the system from what would be predicted from just the stabilities of complementary subsystem pairs. What role do the feedbacks between different subsystems play in influencing the stability of the four empirical systems that exhibit cycles ("unstable" in column 4 of Table 1)? First, the evolutionary subsystem was unstable in all four systems and the complementary ecological subsystem was stable in three of the four systems. For example, in the Becks et al. (3) model, the prey trait diverges from equilibrium when the species' densities are fixed at their equilibrium values (figure 2C) whereas predator and prey densities converge to equilibrium when the prey trait is fixed at its equilibrium density (figure 2B). This means that the feedbacks between the ecological and evolutionary subsystems were insufficiently strong to stabilize the system. Second, the evolutionary and eco-evolutionary subsystems for the victim species were unstable in all four systems and their complementary subsystems were stable in three of four systems. For example, in the Becks et al. (3) model, the prey density and trait diverge from equilibrium when predator density and nutrient concentration are fixed at their equilibrium values (figure 2D). This means that the feedbacks between the victim subsystems and their complementary subsystems were insufficiently strong to stabilize the system. Third, the evolutionary, evolutionary, eco-evolutionary subsystems for

the exploiter species were stable or neutral in three of the studies and their complementary subsystems were stable in all four systems. This means that the feedbacks between the exploiter subsystems and their complementary subsystems were destabilizing and sufficiently strong to alter the stability of the whole system.

What role do the feedbacks between different subsystems play in influencing the stability of the five empirical systems that converge to an equilibrium ("stable" in column 4 of Table 1)? First, in two of the five systems, all of subsystems we considered were stable (21; 10). This means that for all complementary pairs of subsystems we considered, all of the feedbacks between the subsystems were either stabilizing or destabilizing but insufficiently strong to destabilize the whole system. Second, for three of the systems, there was at least one complementary subsystem pair where one of the subsystems was unstable and its complement was stable. This means that for each of these systems, the feedbacks between the complementary subsystems were stabilizing and sufficiently strong to stabilize the whole system. For example, while the prey evolutionary and eco-evolutionary feedbacks were destabilizing in Kasada et al. (27), we predict that the whole system was stable because the feedbacks between those subsystems and their complements were strongly stabilizing.

Effects of evolutionary speed on stability

Our results in the previous section showed that for a subset of our systems the feedbacks between the ecological and evolutionary subsystems altered the stability of the whole system from what would be predicted from just the stabilities of ecological and evolutionary subsystems. Here, we explore how the speed of evolution influences whether the feedbacks between the ecological and evolutionary subsystems alter system stability.

Varying the speed of evolution in the nine parameterized models produced one of four patterns (two shown in figure 3), which help identify how feedbacks between the ecological and evolutionary subsystems and the speed of evolution influence the stability of the whole system. First, for all four systems with stable ecological subsystems and unstable evolu-

tionary subsystems (S-U in "Eco & Evo" column of Table 1), stability of the whole system switched from stable to unstable as the speed of evolution increased. For example, figure 3A-C shows the stability of the Becks et al. (3) model for varied evolutionary speeds. In these systems, the cyclic dynamics in the fast evolution limit are expected due to the instability of the evolutionary subsystem. Stability in the slow evolution limit is caused by stabilizing feedbacks between the ecological and evolutionary subsystems that are sufficiently strong to counteract the instability of the evolutionary subsystem. Hence, feedbacks between the ecological and evolutionary subsystems do not alter the stabilities of these systems in the fast evolution limit, but they do stabilize the systems in the slow evolution limit.

Second, for the Haafke et al. (14) study where the ecological and evolutionary subsystems were both unstable, the whole system exhibited cycles for all evolutionary speeds. The cycles in the slow and fast evolution limits are expected based on the instabilities of the ecological and evolutionary subsystems, respectively. The presence of cycles for all evolutionary speeds implies that the feedbacks between the ecological and evolutionary subsystems did not alter the stability of the system for any speed of evolution.

Third, for three of the four systems where the ecological and evolutionary subsystems were both stable (S-S in "Eco & Evo" column of Table 1), the system was stable for all evolutionary speeds. Stability for all evolutionary speeds implies that the feedbacks between the ecological and evolutionary subsystems did not alter the stability of any of the systems for any speed of evolution.

Fourth, for the final system where the ecological and evolutionary subsystems were both stable (28), the system was stable for very fast and very slow evolutionary speeds and unstable for intermediate evolutionary speeds (figure 3D-F). Stability in the slow and fast evolution limits implies that the feedbacks between the ecological and evolutionary subsystems did not alter the stability of the system when evolution was much slower or faster than ecology. However, instability of the whole system for intermediate evolutionary rates means that the feedbacks between the ecological and evolutionary subsystems were sufficiently strong to

destabilize the system for intermediate speeds of evolution.

Overall, our results showed that the feedbacks between the ecological and evolutionary subsystems could alter system stability for some range of evolutionary speeds in five of the systems (the four with S-U in "Eco & Evo" column of Table 1 and Duffy et al. (28)). In particular for the Duffy et al. (28) model, instability of the eco-evolutionary feedbacks are necessary to predict the instability of the whole system for intermediate speeds of evolution. For the other four systems, the feedbacks between the ecological and evolutionary subsystems were insufficiently strong to counteract the (de)stabilizing effects of the ecological and evolutionary subsystems and alter the stability of the whole system.

Discussion

Our results suggest that ecological, evolutionary, and eco-evolutionary feedbacks have systematically different effects on the stabilities of empirical systems and that those effects may depend on the species trophic level. Across the nine existing examples of empirically parameterized models of eco-evolutionary feedbacks, ecological feedbacks tended to be stabilizing. In contrast, evolutionary feedbacks were stabilizing or destabilizing, with exploiter evolutionary feedbacks being stabilizing or neutral and victim evolutionary feedbacks being evenly split between stabilizing and destabilizing. Exploiter and victim ecological and eco-evolutionary feedbacks also consistently differed, with exploiter eco-evolutionary feedbacks being stabilizing or neutral and victim eco-evolutionary feedbacks being destabilizing more often than stabilizing. While our results are based on all empirically-parameterized models known to the authors, these models only represent a small number of systems, all of which involve exploiter-victim interactions. An important area of future work is applying and testing this theory in empirical systems with interactions other than exploiter-victim to understand whether ecological, evolutionary, and eco-evolutionary feedbacks have similar or different effects on stability in those systems.

Our results help elucidate why some eco-evolutionary systems converge to steady state whereas others exhibit cycles. For all four systems that exhibit cyclic dynamics, the evolutionary subsystem of the victim species was unstable. This implies that disruptive selection was one of the processes driving cycles in those systems. In contrast, in all but one of the systems that converged to steady state, the evolutionary subsystems for the victim species were stable (implying stabilizing selection). This suggests that evolutionary feedbacks were the primary factors determining the stabilities of our nine systems. Stabilizing and disruptive selection are observed with roughly equal frequencies across a broad set of empirical systems (29). In combination with our results, this suggests that the destabilizing effects of evolutionary feedbacks are widespread across empirical systems.

Our results also help identify when eco-evolutionary feedbacks do and do not alter stability. First, in all but one system, the stability of the whole system could be predicted from just the stabilities of the ecological and evolutionary subsystems. This means that in eight of the nine systems, eco-evolutionary feedbacks between all species did not alter the stability of the whole system. The one exception is the Kasada et al. (27) study, where the victim evolutionary subsystem was unstable, but the whole system was stable. For this system, we predict that the eco-evolutionary feedbacks of the system were stabilizing and sufficiently strong to counteract the destabilizing evolutionary feedbacks and stabilize the whole system.

Second, while the eco-evolutionary feedbacks between all species densities and traits were stabilizing, our results show that eco-evolutionary feedbacks involving just a subset of the species in the community could have different effects on stability. In particular, we found that the eco-evolutionary feedbacks between the densities and traits of exploiter species were stabilizing. In contrast, the eco-evolutionary feedbacks between the densities and traits of victim species could be stabilizing or destabilizing. Our results about the destabilizing effects of victim eco-evolutionary feedbacks are consistent with prior theoretical predictions that prey eco-evolutionary feedbacks can be destabilizing (2; 4; 8). While theory predicts predator eco-evolutionary feedbacks can also be destabilizing (30; 26), this was not observed

in the four systems with exploiter evolution.

Our predictions about subsystem stability can be tested in empirical systems through controlled experiments in which some variables are held (nearly) fixed at their equilibrium values. One way to effectively fix evolutionary variables is to seed populations with lower standing genetic variation (e.g., as in Fridley and Grime (31), Becks et al. (3), Turcotte et al. (32), and Crustinger et al. (33)). If the magnitude of genetic variation is varied while the mean trait value is kept (effectively) constant, then the low genetic variation treatment will yield information about the stability of subsystems without that trait. For example, because the rotifer-algae system in Becks et al. (3) was stable when initial algal genetic variation was low and unstable when initial genetic variation was higher, we predict that the ecological subsystem must have been stable and at least one evolutionary or eco-evolutionary subsystem must have been unstable. Similarly, holding a species' density nearly fixed will yield information about the stabilities of subsystems without that species. For example, in predator-prey systems where predator generation times are much longer than prey generation times, experiments where predator densities are held constant will yield information about the eco-evolutionary subsystems involving the prey density and traits.

It is important to note that, in most cases, subsystem stability cannot be determined by experiments where a variable is removed (e.g., removing a predator instead of fixing its density) or changed substantially from its equilibrium value (e.g., using undefended clones as the 'low variation' treatment in the algae example). This is because the subsystem theory assumes all fixed variables are held at their equilibrium values. It may be difficult or infeasible to hold densities or traits (nearly) constant in a given empirical system. Nonetheless, applying our theory to parameterized models tailored to particular systems allows one to make predictions about how specific feedbacks influence community stability and dynamics.

Our results highlight the need for additional theory to explain how rates of evolution (relative to ecological rates) influence system stability. Current theory (8; 26; 16; 15) predicts that system stability in the slow and fast evolution limits is determined, in part, by the

stabilities of the ecological and evolutionary subsystems, respectively. For eight of the nine parameterized models, system stability at all evolutionary speeds matched the stability of either the ecological subsystem or the evolutionary subsystem. However, this does not mean that feedbacks between the ecological and evolutionary subsystems are unimportant for determining system stability. Instead, our results show that eco-evolutionary feedbacks have the potential to alter system stability in half of the systems we considered. First, our results for systems with stable ecological subsystems and unstable evolutionary subsystems (S-U in "Eco & Evo" column of Table 1) show that there is a transition from stability to cycles with faster evolution (Figure 3A-C). For these systems, eco-evolutionary feedbacks must be stabilizing the system when evolution is sufficiently slow. Second, the Duffy et al. (28) model exhibits cycles at intermediate evolutionary speeds even though the ecological and evolutionary subsystems are stable (figure 3D-F). For this system, the cycles must be driven by destabilizing eco-evolutionary feedbacks.

The stability pattern in the Duffy et al. (28) model (cycles at intermediate evolutionary speeds and stability otherwise) has been observed in eco-evolutionary predator-prey models (8; 26; 16). It is predicted to occur when smaller subsystems (involving fewer variables) are weakly stable compared to larger subsystems (involving more variables), or vice versa (16). In effect, subsystems of one size have a small effect on the stability of the whole system, subsystems of a different size have a larger effect, and this asymmetry destabilizes the system at intermediate evolutionary speeds. Because there is only one unstable subsystem in the Duffy et al. (28) model, a similar mechanism may explain figure 3D-F. However, for that system and more generally, there is a need for theory that explains how the strengths of different feedbacks depend on the speed of evolution (15), and how that influences system stability.

Our subsystem-based approach can be extended and potentially fruitful in other areas. First, applying our approach to a particular subsystem can help determine what feedbacks within that subsystem are responsible for its stability. For example, nearly all systems

with unstable victim eco-evolutionary subsystems also had unstable victim evolutionary subsystems. Thus, instability of those eco-evolutionary subsystems must be due, in part, to the destabilizing effects of evolutionary feedbacks of the victim species. Second, following Cortez (16), the approach can also be extended to consider the effects of all subsystems. However, in systems with many species, all of which may be potentially evolving, the number of subsystems becomes very large, e.g, the Wei et al. (34) model with 10 variables has 1023 subsystems. Thus, new theory is needed to help understand what general rules govern how and when different subsystems influence system stability. Third, our approach may also be useful in purely ecological contexts. For example, our approach could help identify how behavioral dynamics and species abundance dynamics affect community stability, how feedbacks within and between trophic levels affect the stability of food webs, how within-soil and above-soil communities contribute to the stability of plant-soil communities, and how environmental dynamics and species abundance dynamics affect system stability.

By applying our method to the nine currently available empirical models with eco-evolutionary feedbacks, we uncovered surprising patterns on the role of ecological and evolutionary processes and their interactions in shaping the dynamics of empirical systems. Looking forward, as eco-evolutionary feedbacks are detected in more experimental and natural systems, we can continue to apply our method and test whether the patterns we observe are common across empirical systems.

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Tables and Figures

Table 1: Effects of complementary pairs of subsystems on system stability in parameterized models from the literature

Study	Evolving Species	System Stability	Stabilities of complementary subsystem pairs*				
			Eco & Evo	Prey evo	Prey eco or eco-evo†	Pred Evo	Pred eco or eco-evo†
Predator-prey							
Becks et al. (3)	Prey	Unstable	S - U	U - S	U - S		S - U
Frickel et al. (10)	Both	Stable	S - S	S - S	S - S	S - S	S - S
Haafke et al. (14)	Both	Unstable	U - U	U - U	U - S	S - U	S - U
Kasada et al. (27)	Prey	Stable	S - U	U - S	U - S		N - U
Wei et al. (34) Fig. 5a	Both	Stable	S - S	S - S	S - S	N - S	N - S
Fig. 5b	Both	Stable	S - S	S - U	U - S	N - S	N - U
Yoshida et al. (12; 11)	Prey	Unstable	S - U	U - S	U - S		N - U
Intraguild predation							
Hiltunen et al. (35)‡ Fig. 2.1b	Basal prey	Unstable	S - U	U - S	U - S		S - U
Fig. 2.1c	Basal prey	Unstable	S - U	U - S	U - U		U - U
Fig. 2.1d	Basal prey	Unstable	S - U	U - S	U - S		S - U
Host-parasite							
Bolker et al. (21)	Parasite	Stable	S - S		S - S	S - S	S - S
Duffy et al. (28)	Host	Stable	S - S	S - S	S - S		U - S

* The first and second letters define how the subsystem listed in the column and its complementary subsystem, respectively,

affect the stability of the whole system (S= stabilizing, U = destabilizing, N = neutral effect, Eco = ecological, Evo = evolutionary, Eco-evo = eco-evolutionary).

† In systems without victim (exploiter) evolution, the victim (exploiter) eco-evolutionary and ecological systems are the same.

‡ Victim subsystems only involve the basal prey variables and exploiter subsystems involve the intraguild prey and intraguild predator variables.

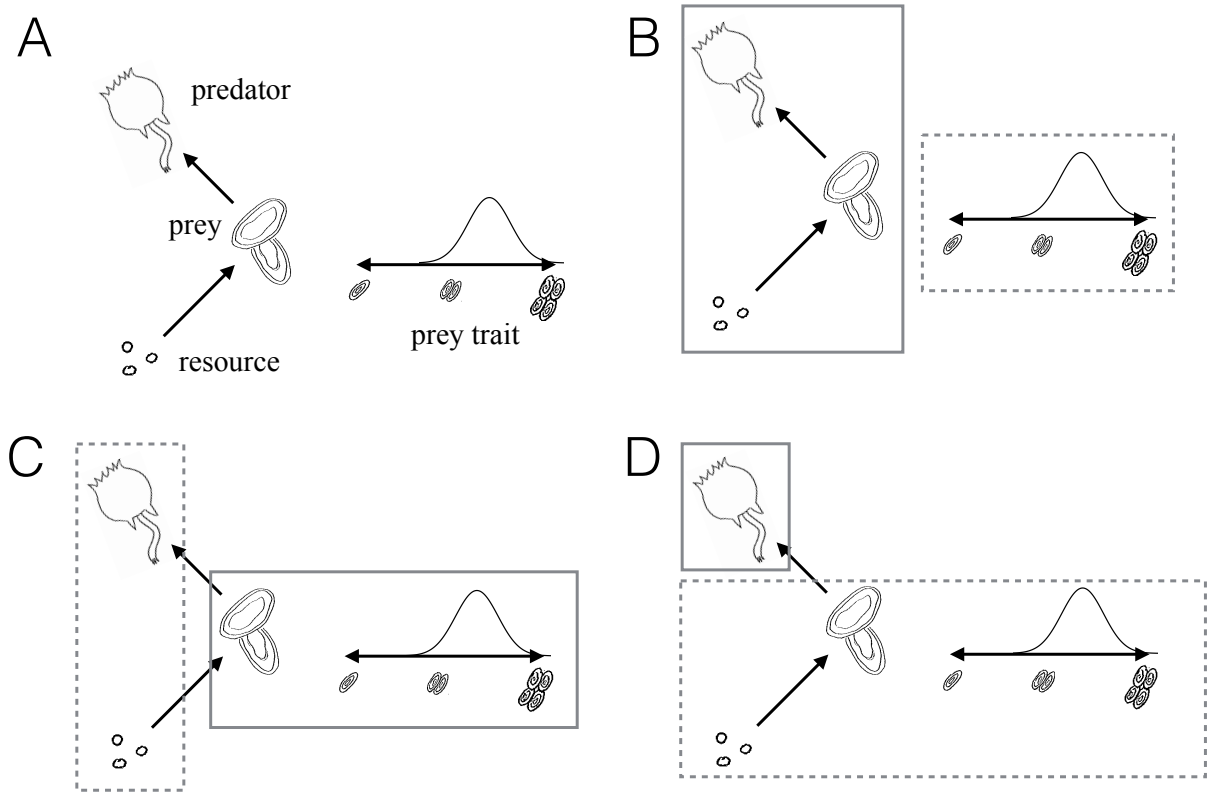

Figure 1: Examples of complementary subsystem pairs in the resource-prey-predator system with an evolving prey trait from Becks et al. (3). (A) The system dynamics involve changes in resource (nitrogen), prey (algae), and predator (rotifers) densities and the mean clump size of the prey. (B) Ecological subsystem (solid box) and its complementary evolutionary subsystem (dashed box). (C) Prey eco-evolutionary subsystem (solid box) and its complementary subsystem (dashed box). (D) Predator ecological subsystem (solid box) and its complementary subsystem (dashed box).

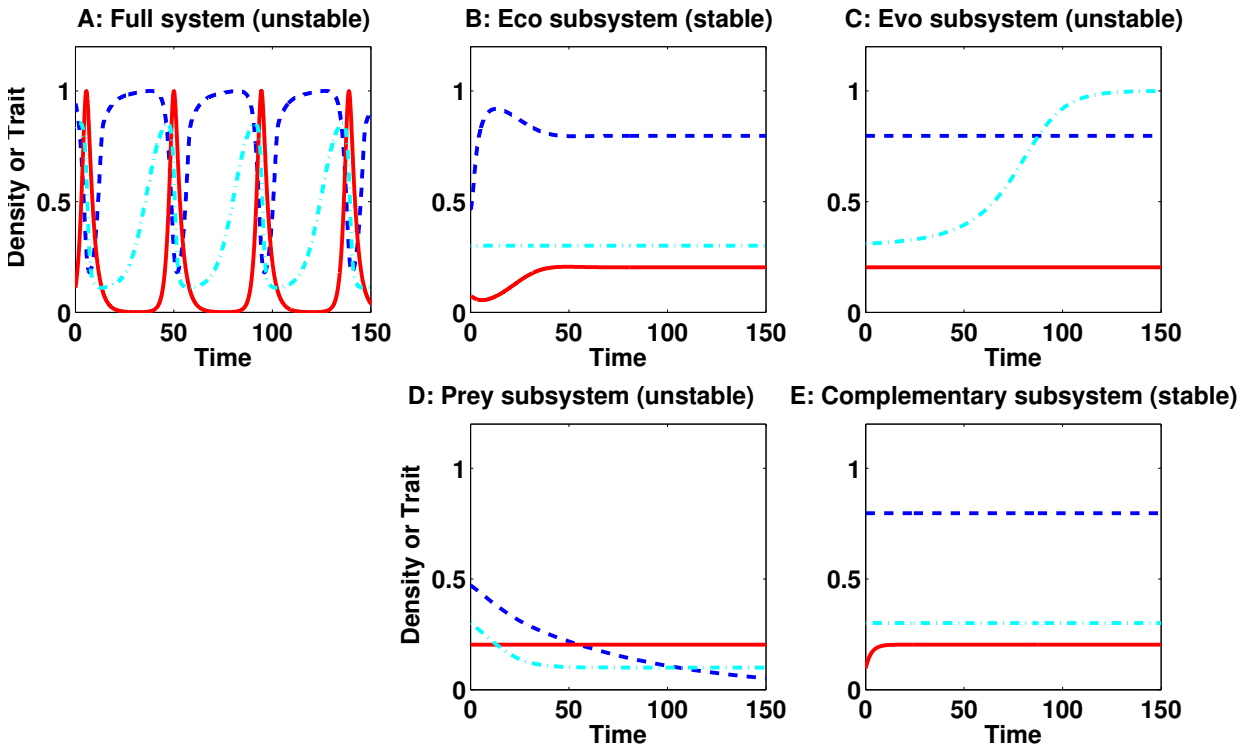

Figure 2: Dynamics and stabilities of the subsystems of the eco-evolutionary predator-prey model in Becks et al. (3). All panels show scaled prey (dashed blue) and predator (solid red) densities and the proportion of defended prey (dash dot cyan); nutrient dynamics are not shown. (A) The equilibrium of the whole system is unstable, which yields eco-evolutionary cycles. (B) The ecological subsystem is stable: when the prey trait is held at its equilibrium value, all species densities converge to their equilibrium values. (C) The (prey) evolutionary subsystem is unstable: when the species densities are held at their equilibrium values, the prey trait diverges from its equilibrium value. (D) The prey eco-evolutionary subsystem is unstable: when nutrient and predator densities are held at their equilibrium values, the prey trait and prey density diverge from their equilibrium values. (E) The complement of the prey eco-evolutionary subsystem is stable: when the prey density and trait are held at their equilibrium values, the nutrient and predator densities converges to their equilibrium values.

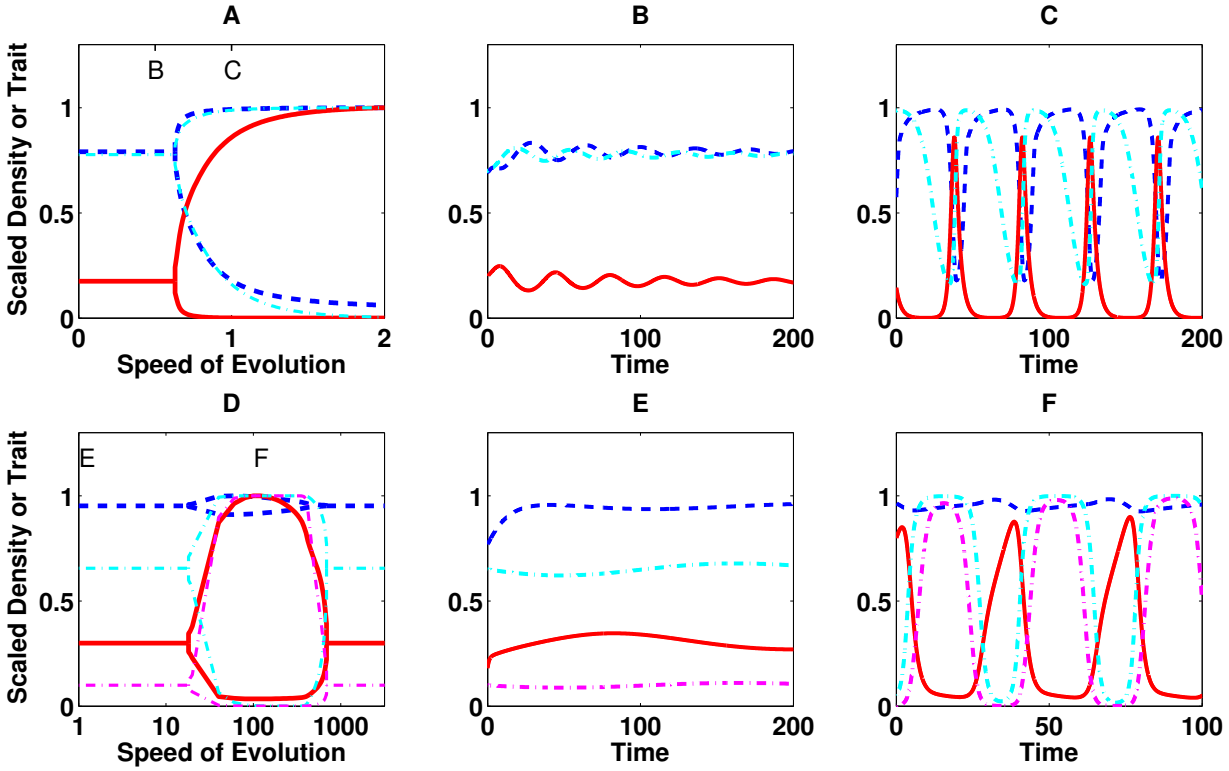

Figure 3: Predicted stability and dynamics of eco-evolutionary models with increased or decreased rates of evolution. (A-C) Dynamics of the Becks et al. (3) model with prey density (dashed blue), predator density (solid red), and proportion of defended prey (dash-dot cyan); nutrient dynamics are not shown. (D-F) Dynamics of the Duffy et al. (28) model with susceptible host density (dashed blue), infected host density (solid red), and proportions of resistant susceptible and infected hosts (dash-dot cyan and magenta, respectively). (A,D) Maximum and minimum long-term values for different evolutionary speeds; a single curve for each variable denotes the stable equilibrium value whereas two curves denote the maximum and minimum values during eco-evolutionary cycles. An evolutionary speed of one denotes the speed of evolution for the estimated parameter values in the original study. Letters denote evolutionary speeds for other panels.

Supplementary Information

'Destabilizing evolutionary and eco-evolutionary feedbacks drive eco-evo cycles in empirical systems'

Michael H. Cortez, Swati Patel, and Sebastian J. Schreiber

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S1 Notation and complementary subsystem method

To simplify notation, let $\vec{N} = (N_1, ..., N_n)$ be the vector of species densities and $\vec{x} = (x_1, ..., x_m)$ be the vector of evolving traits. Let $\rho = (\vec{N}^*, \vec{x}^*)$ denote a coexistence equilibrium of the model from the main text, i.e., an equilibrium where all species have nonzero densities. When evaluated at ρ, the Jacobian of the model has the form

$$
\begin{aligned}
J|_\rho &= \begin{pmatrix}
J_{1,1} & \cdots & J_{1,n} & J_{1,n+1} & \cdots & J_{1,n+m} \\
\vdots & \ddots & \vdots & \vdots & & \vdots \\
J_{n,1} & \cdots & J_{n,n} & J_{n,n+1} & \cdots & J_{n,n+m} \\
J_{n+1,1} & \cdots & J_{n+1,n} & J_{n+1,n+1} & \cdots & J_{n+1,n+m} \\
\vdots & & \vdots & \vdots & \ddots & \vdots \\
J_{n+m,1} & \cdots & J_{n+m,n} & J_{n+m,n+1} & \cdots & J_{n+m,n+m}
\end{pmatrix} \\
&= \begin{pmatrix}
N_1 \partial f_1/\partial N_1 & \cdots & N_1 \partial f_1/\partial N_n & N_1 \partial f_1/\partial x_1 & \cdots & N_1 \partial f_1/\partial x_m \\
\vdots & \ddots & \vdots & \vdots & & \vdots \\
N_n \partial f_n/\partial N_1 & \cdots & N_n \partial f_n/\partial N_n & N_n \partial f_n/\partial x_1 & \cdots & N_1 \partial f_n/\partial x_m \\
\partial g_1/\partial N_1 & \cdots & \partial g_1/\partial N_n & \partial g_1/\partial x_1 & \cdots & \partial g_1/\partial x_m \\
\vdots & & \vdots & \vdots & \ddots & \vdots \\
\partial g_m/\partial N_1 & \cdots & \partial g_m/\partial N_n & \partial g_m/\partial x_1 & \cdots & \partial g_m/\partial x_m
\end{pmatrix}.
\end{aligned}
\tag{S.1}
$$

The diagonal entries for the first n rows have been simplified using $f_i(\rho) = 0$. The equilibrium point is stable if all eigenvalues of J have negative real parts, neutrally stable if all eigenvalues have non-positive real parts and at least one eigenvalue has negative real part, neutral if all eigenvalues have zero real parts, and unstable if at least one eigenvalue has positive real part.

Let S be a subsystem containing variables $\{s_1, s_2, ..., s_k\}$. Let M_S be the submatrix of J made up of all entries $\partial \dot{s}_i / \partial s_j$. The stability of subsystem S when all variables not contained in S are fixed at their equilibrium values (defined by ρ) is determined by the eigenvalues of

M_S following the same rules used for the full system. Ecological subsystems contain only ecological variables (N_i). Evolutionary subsystems contain only evolutionary variables (x_j). Eco-evolutionary variables contain ecological and evolutionary variables. Two subsystems S_1 and S_2 form a complementary pair if their intersection is the empty set and their union contains all variables in the system. For example, the ecological subsystem contains the variables $S_1 = \{N_1, ..., N_n\}$ and its stability is determined by the submatrix defined by all entries in the first n rows and n columns of J. Its complementary subsystem is the evolutionary subsystem, which contains the variables $S_2 = \{x_1, ..., x_m\}$ and whose stability is determined by the submatrix defined by all entries in the last m rows and m columns of J.

In general, the stabilities of the subsystems influence the stability of the whole system. We begin by illustrating this in a two-dimensional system and then show how the idea holds for higher-dimensions. For example, consider a model with one ecological variable (N) and one evolutionary variable (x). Such a model has a 2x2 Jacobian (J) where the stability of the ecological subsystem is determined by the J_{11} entry, the stability of the evolutionary subsystem is determined by the J_{22} entry, and the interactions between the subsystems are defined by the product $J_{12}J_{21}$. When $J_{11} < 0$, the ecological subsystem has a stabilizing effect on the stability of the whole system and when $J_{11} > 0$, the ecological subsystem has a destabilizing effect on the stability of the whole system. Similarly, when $J_{22} < 0$ the evolutionary subsystem has a stabilizing effect on the stability of the whole system and when $J_{22} > 0$ the evolutionary subsystem has a destabilizing effect on the stability of the whole system. In the absence of bidirectional feedbacks between the ecological and evolutionary subsystem (i.e., $J_{12}J_{21} = 0$), the stability of the whole system is determined by the stability of the ecological and evolutionary subsystems. However, when bidirectional feedbacks are present, the interactions between the two subsystems have stabilizing effects when $J_{12}J_{21} > 0$ and destabilizing effects when $J_{12}J_{21} < 0$.

A similar idea holds in higher dimensional models, where the entries J_{11} and J_{22} are re-

placed by submatrices of the Jacobian corresponding to a pair of complementary subsystems. The entries J_{12} and J_{21} are replaced by submatrices that represents the feedbacks between the subsystems. Thus, stability of the whole system is affected by the stability of each subsystem as well as the feedbacks between the subsystems. While we have focused on particular biologically-motivated pairs of complementary subsystems, there are a combinatorially many number of subsystems that influence the stability of the whole system.

To show how stable, neutrally stable, and neutral subsystems influence system stability in higher dimensions, we use use the characteristic polynomial of the Jacobian. As an example consider a four dimensional system with variables N_1, N_2, N_3 and x_1. The characteristic polynomial of the Jacobian (J) for such a system is

$$p(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 \tag{S.2}$$

where

$$\begin{aligned}
a_1 &= -(|M_{N_1}| + |M_{N_2}| + |M_{N_3}| + |M_{x_1}|) \\
a_2 &= |M_{N_1N_2}| + |M_{N_1N_3}| + |M_{N_1x_1}| + |M_{N_2N_3}| + |M_{N_2x_1}| + |M_{N_3N_1}| \\
a_3 &= -(|M_{N_1N_2N_3}| + |M_{N_1N_2x_1}| + |M_{N_1N_3x_1}| + |M_{N_2N_3x_1}|) \\
a_4 &= |J|
\end{aligned} \tag{S.3}$$

and $|\cdot|$ denotes the determinant of a (sub)matrix. A necessary condition for system stability is all coefficients of the characteristic polynomial are positive, i.e., $a_i > 0$ for all i. To see how the ecological subsystem (i.e., the N_1, N_2, N_3-subsystem) affects the stability of the whole system, consider the characteristic polynomial for the submatrix $M_{N_1N_2N_3}$,

$$q(\lambda) = \lambda^3 + b_1\lambda^2 + b_2\lambda + b_3 \tag{S.4}$$

where

$$
\begin{aligned}
b_1 &= -(|M_{N_1}| + |M_{N_2}| + |M_{N_3}|) \\
b_2 &= |M_{N_1N_2}| + |M_{N_1N_3}| + |M_{N_2N_3}| \\
b_3 &= -|M_{N_1N_2N_3}|.
\end{aligned}
\tag{S.5}
$$

A necessary condition for stability of the ecological subsystem is $b_i > 0$ for all i. Notice that each term in the b_1 equation also shows up in the equation for a_1. The same holds for the b_2 and a_2 equations and the b_3 and a_3 equations. Thus, b_i is a partial sum of the terms that define a_i.

If the ecological subsystem is unstable, then at least one of the b_i coefficients is negative. Because b_i is a partial sum of the terms that define a_i, if b_i is a negative value, then a_i will be a more negative (or less positive) value. In terms of satisfying the necessary condition for stability of the whole system ($a_i > 0$), this means that an unstable ecological subsystem has a destabilizing effect on the stability of the whole system. In contrast, stable ecological subsystems ($b_i > 0$ for all i), neutrally stable ecological subsystems ($b_i \geq 0$ for all i, with at least one of the b_i coefficients being positive), or neutral ecological subsystems with purely imaginary eigenvalues (also $b_i \geq 0$ for all i, with at least one of the b_i coefficients being positive) have stabilizing effects on the whole system because the a_i coefficients are more positive if some of the b_i are positive. For neutral ecological subsystems where all eigenvalues are zero ($b_i = 0$ for all i), the subsystem has no direct effect on the stability of the whole system. For all of the models we examined, every neutral subsystem only had zero eigenvalues.

The above argument holds for a Jacobian of any size and a submatrix of any size. It explains our interpretation of how subsystems with different stabilities affect the stability of the whole system. The above only focuses on the necessary condition for (sub)system stability, i.e., all coefficients of the characteristic polynomial are positive. Necessary and sufficient conditions for stability are defined by the Routh-Hurwitz criteria. We do not use the conditions from the Routh-Hurwitz criteria because they are more complex and less

tractable for large matrices.

S2 Converting discrete trait models into continuous trait models

To apply our theory to the parameterized clonal models from the literature, we converted the (discrete trait) clonal models into continuous trait models. The simplest models had no stage structure and two clones with densities C_1 and C_2. These models were transformed into continuous trait models using $C = C_1 + C_2$ and $x_1 = C_1/C$, where the trait is the proportion of clone 1. For clonal models without stage structure and $k > 2$ clones with densities $C_1, C_2, C_3, ..., C_k$, the variables of the continuous trait models are $C = C_1 + \cdots + C_k$ and $x_j = C_j/C$ for $j < k$. This yields one ecological variable and $k-1$ evolutionary variables defined as the proportions of clone j ($j < k$). For clonal models with stage structure, the traits are the proportions of one clone in each stage. For example, for clonal densities C_1, C_2 in stage 1 and D_1, D_2 in stage 2, the variables of the continuous trait model are $C = C_1 + C_2$, $D = D_1 + D_2$, $x_1 = C_1/C$ and $x_2 = D_1/D$.

S3 Varying evolutionary speeds in continuous trait models

To vary the speed of evolution in the models, we multiplied the right hand sides of the trait equations by the parameter ϵ_i, where the rate of evolution is unchanged for $\epsilon_i = 1$ and is slowed down (sped up) for $0 < \epsilon_i < 1$ ($\epsilon_i > 1$). For example, the trait dynamics $dx_1/dt = g(\cdot)$ are changed to $dx_1/dt = \epsilon_1 g(\cdot)$. For systems where a single species had multiple traits, each trait equation was multiplied by the same parameter (e.g., ϵ_1 for all trait equations). For systems with multiple evolving species, the trait equations for different species were multiplied by different parameters (e.g., ϵ_1 for the prey trait and ϵ_2 for the predator trait).

Our analysis only focused on the effects of varying each ϵ_i parameter independently; we did not explore how simultaneously varying multiple ϵ_i parameters would affect system stability.

Multiplying a trait equation by ϵ_i results in each entry of the Jacobian corresponding to that trait equation being multiplied by ϵ_i. Thus, varying ϵ_i changes the magnitudes of those Jacobian entries, which in turn affects the eigenvalues of the Jacobian. For all of the models we considered, changing the rate of evolution (i.e., varying ϵ_i) does not change the location of an equilibrium point. Thus, varying ϵ_i does not affect the entries of the Jacobian corresponding to the ecological equations or other trait equations. In addition, for all models we considered, equilibria can only undergo Hopf bifurcations as the ϵ_i parameters are varied (15). Moreover, it is not possible for the equilibrium to undergo any bifurcation where one or more eigenvalues are identically zero. The reason is that the determinant of the Jacobian factors as $|J| = \epsilon_i |J_{\epsilon_i=1}|$ where $|J_{\epsilon_i=1}|$ is the determinant of the Jacobian when $\epsilon_i = 1$. Recall that the determinant of a matrix is equal to the product of its eigenvalues. Thus, if the equilibrium were to undergo a bifurcation with a zero eigenvalue, then $|J_{\epsilon_i=1}| = 0$ and the Jacobian would have a zero eigenvalue for all ϵ_i values. Overall, this means that increasing or decreasing the rate of evolution can either cause no effect on stability, cause a system undergoing oscillations to converge to an equilibrium (stabilization), or cause a stable system to exhibit cycles (destabilization).

S4 Analysis of parameterized models

For each model we present (1) the original model and parameter values, (2) the transformations used to convert clonal models to continuous trait models, (3) the Jacobian for the continuous trait model, and (4) the variables in each complementary subsystem pair. We refer the reader to the original studies for information about parameters and functional forms. The stabilities for all subsystem pairs are given in table S1.

All calculations can be reproduced using the accompanying Maple worksheet. The Jaco-

bian and the stabilities of the subsystems for each model can also be reproduced using the accompanying R files, however the results for subsystem stability differ between the Maple worksheet and R files. All differences are due to small numerical errors in R where R computes non-zero values for some entries of the Jacobian that are analytically zero. If these numerical errors are accounted for (i.e., the entries are set equal to zero), then the results from R and Maple agree. In the following, Jacobian entries are listed as zero only if it is possible to show analytically that the entry is zero (see Maple worksheet for details). All other entries are taken from the Maple worksheet and rounded to three significant digits.

Table S1: Stabilities of complementary pairs of subsystems in parameterized models from the literature

Study	Evolving Species	System Stability	Stabilities of complementary subsystem pairs*				
			Eco & Evo	Prey evo	Prey eco or eco-evo†	Pred Evo	Pred eco or eco-evo†
Predator-prey							
Becks et al. (3)	Prey	Unstable	S - U	U - S	U - NS		NS - U
Frickel et al. (10)	Both	Stable	S - S	S - S	NS - NS	S - S	NS - S
Haafke et al. (14)	Both	Unstable	U - U	U - U	U - NS	NS - U	NS - U
Kasada et al. (27)	Prey	Stable	S - U	U - S	U - NS		N - U
Wei et al. (34) Fig. 5a	Both	Stable	S - S	S - NS	S - NS	N - S	N - S
Fig. 5b	Both	Stable	S - S	S - U	U - NS	N - S	N - U
Yoshida et al. (12; 11)	Prey	Unstable	S - U	U - S	U - NS		N - U
Intraguild predation							
Hiltunen et al. (35)‡ Fig. 2.1b	Basal prey	Unstable	S - U	U - S	U - S		S - U
Fig. 2.1c	Basal prey	Unstable	S - U	U - S	U - U		U - U
Fig. 2.1d	Basal prey	Unstable	S - U	U - S	U - S		S - U
Host-parasite							
Bolker et al. (21)	Parasite	Stable	S - S		S - NS	S - S	NS - S
Duffy et al. (28)	Host	Stable	S - S	S - S	S - S		U - S

* The first letter is the stability of the subsystem listed in the column and the second is the stability of the complementary subsystem. S = all eigenvalues for the submatrix have negative real part; U = at least one eigenvalue has positive real

part; NS = at least one eigenvalue has negative real part and at least one eigenvalue is zero; N = all eigenvalues are zero. Eco = ecological subsystem; Evo = evolutionary subsystem; Eco-evo = eco-evolutionary subsystem; Pred = exploiter (predator or pathogen); Prey = victim (prey or host).

† For systems without prey (predator) evolution, the prey (predator) eco-evolutionary subsystem is just the prey (predator) ecological subsystem.

‡ Prey subsystems refer to subsystems with just the basal resource variables and predator subsystems refer to subsystems with both the intraguild prey and the intraguild predator variables.

S4.1 Becks et al. (3) Model

The model is

$$
\begin{aligned}
\frac{dN}{dt} &= \delta(N_I - N) - \frac{\rho C_1 N}{K_{c,1} + N} - \frac{\rho C_2 N}{K_{c,2} + N} \\
\frac{dC_i}{dt} &= \frac{\chi_c \rho N C_i}{K_{c,i} + N} - \frac{p_i G (B+S) C_i}{K_B + Q} - \delta C_i \\
\frac{dB}{dt} &= \frac{p_i G B Q}{K_B + Q} - (\delta + m + \lambda) B \\
\frac{dS}{dt} &= \lambda B - (\delta + m) S
\end{aligned}
\tag{S.6}
$$

where N is the concentration of nitrogen, C_i is the density of algal clones ($i = 1, 2$), B and S are the densities of breeding and senescent rotifers, and $Q = p_1 C_1 + p_2 C_2$. The parameter values are $p_2 = 1$, $N_I = 160$, $\delta = 0.3$, $m = 0.055e$, $\lambda = 0.4$, $\chi_c = 0.0027$, $K_{c,2} = 2.2$, $K_{c,1} = 8 - 5.8p_1$, $\rho = 270$, $\chi_B = 170$, $K_B = 0.15$, $G = 0.011$, $p_1 = 0.1$.

The four ecological variables for the continuous trait model are N, $C = C_1 + C_2$, B, and S, and the single evolutionary variable is $x_1 = C_1/C$. The Jacobian for the continuous trait model is

$$
\begin{pmatrix}
-3.94 & -137 & 0 & 0 & -26.0 \\
0.00983 & 0.028 & -0.00444 & -0.00444 & -0.0284 \\
0 & 3.31 & 0 & 0 & -3.35 \\
0 & 0 & 0.4 & -0.355 & 0 \\
0.00105 & -0.0431 & 0.00682 & 0.00682 & 0.0436
\end{pmatrix}
\tag{S.7}
$$

where the order of the rows and columns is (N, C, B, S, x_1). The ecological subsystem is $\{N, C, B, S\}$ and the complementary evolutionary subsystem is $\{x_1\}$; this pair of subsystems also defines the prey evolutionary subsystem and its complement. The prey eco-evolutionary subsystem and its complement are $\{C, x_1\}$ and $\{N, B, S\}$. The predator ecological subsystem and its complement are $\{B, S\}$ and $\{N, C, x_1\}$.

S4.2 Bolker et al. (21) Model

The model is

$$\begin{aligned} \frac{dS}{dt} &= m(N-S) - \beta(\alpha)SI \\ \frac{I}{dt} &= \beta(\alpha)SI - (m+\alpha)I \\ \frac{d\alpha}{dt} &= V_g\left(S\frac{d\beta}{d\alpha} - 1\right) \end{aligned} \tag{S.8}$$

where S is the density of susceptible hosts, I is the density of infected hosts, and α is the population mean virulence of the pathogen; S and I are ecological variables and α is the evolutionary variable. The transmission rate is defined by $\beta(\alpha) = c\alpha^{1/\gamma}$. Multiple parameterizations are provided for this model because it was applied to four different disease systems. (The values of c and γ are computed from the reported values of R_0 and α^*; see original study for details). The parameters for SARS were $N = 1$, $m = 1$, $c = 4.45$, $\gamma = 1.156$. The parameters for HIV were $N = 1$, $m = 1$, $c = 2.13$, $\gamma = 1.157$. The parameters for West Nile Virus (WNV) were $N = 1$, $m = 1$, $c = 3.23$, $\gamma = 1.002$. The parameters for Myxomatosis (Myx) were $N = 1$, $m = 1$, $c = 4.71$, $\gamma = 1.2$.

The Jacobians for the different parameterizations are

$$J_{SARS} = \begin{pmatrix} -3 & -641 & -0.09 \\ 2 & 0 & 0 \\ 3 & 0 & -2.43\cdot 10^{-6} \end{pmatrix}, \quad J_{HIV} = \begin{pmatrix} -1.43 & -7.36 & -0.0409 \\ 0.43 & 0 & 0 \\ 1.43 & 0 & -0.0214 \end{pmatrix} \tag{S.9}$$

$$J_{WNV} = \begin{pmatrix} -3.24 & -640 & -0.00108 \\ 2.24 & 0 & 0 \\ 3.24 & 0 & -2.45\cdot 10^{-6} \end{pmatrix}, \quad J_{Myx} = \begin{pmatrix} -3 & -6 & -0.111 \\ 2 & 0 & 0 \\ 3 & 0 & -0.0333 \end{pmatrix}. \tag{S.10}$$

where the orders of the columns and rows are (S, I, α). The ecological subsystem is $\{S, I\}$ and the complementary evolutionary subsystem is $\{\alpha\}$; this pair of subsystems also defines

the parasite evolutionary subsystem and its complement. The parasite eco-evolutionary subsystem and its complement are $\{I, \alpha\}$ and $\{S\}$.

S4.3 Duffy et al. (28) Model

The model is

$$\begin{aligned}
\frac{dS_i}{dt} &= b_i(S_i + fI_i)\left(1 - \frac{\sum_j S_j + I_j}{K}\right) - nS_i - mS_i - \beta_i S_i Z \\
\frac{dI_i}{dt} &= \beta_i S_i Z - nI_i - vI_i - \theta m I_i \\
\frac{d\alpha}{dt} &= -dZ + \sigma(n + v + e\theta m)\left(\sum_j I_j\right) - \sum_j \beta_j S_j Z
\end{aligned} \tag{S.11}$$

where S_i and I_i are the densities of susceptible and infected clonal hosts ($i = 1, 2$), respectively, and Z is the spore density. The parameter values for the model are $b_1 = 5712.11\beta_1 + 0.241$, $b_2 = 5712.11\beta_2 + 0.241$, $d = 0.05$, $e = 0.5$, $f = 0.75$, $K = 5$, $m = 0.1$, $n = 0.05$, $v = 0.05$, $\beta_1 = 0.5 \cdot 10^{-6}$, $\beta_2 = 8.5 \cdot 10^{-6}$, $\theta = 9$, $\sigma = 15000$.

The three ecological variables for the continuous trait model are $S = S_1 + S_2$, $I = I_1 + I_2$, and Z and the evolutionary variables are the proportions of host clone one in each stage, $x_1 = S_1/S$ and $x_2 = I_2/I$. The Jacobian for the continuous trait system is

$$\begin{pmatrix}
-0.0995 & 0.0353 & -6.061340770 \cdot 10^{-6} & 0.00838 & -0.000533 \\
0.0134 & -1 & 6.061340770 \cdot 10^{-6} & -0.0614 & 0 \\
-0.0134 & 8250 & -0.05 & 0.0614 & 0 \\
0.00294 & -0.0383 & 1.806 \cdot 10^{6} & -0.00318 & 0.00171 \\
0 & 0 & 0 & 0.401 & -1
\end{pmatrix} \tag{S.12}$$

where the order of the rows and columns is (S, I, Z, x_1, x_2). For this matrix, all subsystems are stable. The ecological subsystem is $\{S, I, Z\}$ and the complementary evolutionary subsystem is $\{x_1, x_2\}$; this pair of subsystems also defines the prey evolutionary subsystem and its

complement. The prey eco-evolutionary subsystem and its complement are $\{S, I, x_1, x_2\}$ and $\{Z\}$. The parasite ecological subsystem and its complement are $\{I, Z\}$ and $\{S, x_1, x_2\}$.

S4.4 Frickel et al. (10) Model

In matrix form the model is

$$\begin{aligned}
\frac{dS}{dt} &= D(S_0 - S) - c\sum_{i=1}^{N} g_i(S)B_i \\
\frac{d\vec{B}}{dt} &= M_B(g(S) * \vec{B}) - (\phi A\vec{P}) * \vec{B} - D\vec{B} \\
\frac{d\vec{P}}{dt} &= M_p\beta(\phi A^{\mathrm{T}}\vec{B}) * \vec{P} - (\phi A\vec{B}) * \vec{P} - D\vec{P}
\end{aligned} \tag{S.13}$$

where S is the resource concentration, $\vec{B} = (B_1, B_2, B_3, B_4)$ is the density of algal clones, and $\vec{P} = (P_1, P_2, P_3)$ is the density of viral types. In the model, $*$ denotes component-wise multiplication, $g_i(S) = a_i S/(H + S)$, $a_i = a_1 + (a_N - a_1)(i - 1)/(N - 1)$, and A is an upper triangular 4x3 matrix with ones on and above the main diagonal. The matrices M_B and M_p are

$$M_B = \begin{pmatrix} 1-\varepsilon & \varepsilon/2 & 0 & 0 \\ \varepsilon & 1-\varepsilon & \varepsilon/2 & 0 \\ 0 & \varepsilon/2 & 1-\varepsilon & \varepsilon \\ 0 & 0 & \varepsilon/2 & 1-\varepsilon \end{pmatrix}, \quad M_P = \begin{pmatrix} 1-\varepsilon & \varepsilon/2 & 0 \\ \varepsilon & 1-\varepsilon & \varepsilon \\ 0 & \varepsilon/2 & 1-\varepsilon \end{pmatrix} \tag{S.14}$$

The parameter values are $a_1 = 0.25$, $a_N = 0.15$, $D = 0.1$, $S_0 = 30$, $H = 1$, $c = 2.3 \cdot 10^{-5}$, $\phi = 7.5 \cdot 10^{-8}$, $\beta = 100$, $\varepsilon = 10^{-3}$.

The three ecological variables for the continuous trait model are S, total algal density ($B = B_1 + B_2 + B_3 + B_4$), and total viral density ($P = P_1 + P_2 + P_3$). The evolutionary

variables are $x_1 = B_1/B$, $x_2 = B_2/B$, $x_3 = B_3/B$, $x_4 = P_1/P$, $x_5 = P_2/P$. The Jacobian when $\epsilon_4 = 1$ is

$$\begin{pmatrix} -0.564 & 2.32 \cdot 10^{-6} & 0 & -1.85 & -1.24 & -0.618 & 0 & 0 \\ 20200 & 0 & -0.00101 & 80.1 & -26800 & -53300 & 187 & 181 \\ 0 & 0.0736 & 0 & 7.97 \cdot 10^{6} & 7.97 \cdot 10^{6} & 7.93 \cdot 10^{6} & -18500 & -17900 \\ 0.0000967 & 0 & -6.56 \cdot 10^{-10} & -1.18 \cdot 10^{-6} & 0.000268 & 0.00039 & -1.37 \cdot 10^{-6} & -1.32 \cdot 10^{-6} \\ 7.93 \cdot 10^{-7} & 0 & -5.38 \cdot 10^{-12} & 0.000167 & -0.0222 & 6.44 \cdot 10^{-5} & 4.83 \cdot 10^{-6} & -1.09 \cdot 10^{-8} \\ 2.44 \cdot 10^{-5} & 0 & -1.656 \cdot 10^{-10} & -0.0001 & 0.000022 & -0.0441 & 0.000149 & 0.000149 \\ 0 & 0 & 0 & 2.26 \cdot 10^{-5} & -6.46 \cdot 10^{-5} & -8.69 \cdot 10^{-5} & -0.0208 & 4.06 \cdot 10^{-5} \\ 0 & 0 & 0 & 0.00897 & 0.00897 & -0.0356 & 0.000083 & -0.0201 \end{pmatrix} \tag{S.15}$$

where the order of the columns and rows is $(S, B, P, x_1, x_2, x_3, x_4, x_5)$. The ecological subsystem is $\{S, B, P\}$ and the complementary evolutionary subsystem is $\{x_1, x_2, x_3, x_4, x_5\}$. The prey evolutionary subsystem and its complement are $\{x_1, x_2, x_3\}$ and $\{S, B, P, x_4, x_5\}$. The prey eco-evolutionary subsystem and its complement are $\{B, x_1, x_2, x_3\}$ and $\{S, P, x_4, x_5\}$. The predator evolutionary subsystem and its complement are $\{x_4, x_5\}$ and $\{S, B, P, x_1, x_2, x_3\}$. The predator eco-evolutionary subsystem and its complement are $\{P, x_4, x_5\}$ and $\{S, B, x_1, x_2, x_3\}$.

S4.5 Haafke et al. (14) Model

The model is

$$\begin{aligned} \frac{dN}{dt} &= \delta(N_{\text{stock}} - N) - \sum_i \frac{p_i^j A_i N}{K_A^i + N} \\ \frac{dA_i}{dt} &= A_i \left[\frac{X_A p_i N}{K_A^i + N} - \sum_j \frac{p_i^j G(R_j + S_j)}{K_R^j + Q^j} - \delta \right] \\ \frac{dR_j}{dt} &= R_j \left[\frac{X_r G Q^j}{K_R^j + Q^j} - (m + \delta + \lambda) \right] \\ \frac{dS_j}{dt} &= \lambda R_j - (\delta + m) S_j \end{aligned} \tag{S.16}$$

where N is the concentration of nitrogen, A_i is the density of algal clones ($i = 1, 2$), R_j and S_j are the densities of breeding and senescent rotifer clones ($j = 1, 2$), and $Q^j = p_1^j A_1 + p_2^j A_2$. The parameter values are $\delta = 0.3$, $N_{\text{stock}} = 160$, $K_A^1 = 8$, $K_A^2 = 2.2$, $K_R^1 = 0.15$, $K_R^2 = 0.15$, $X_A = 0.0027$, $G = 0.011$, $m = 0.055$, $\lambda = 0.4$, $X_r = 170$, $p_1^1 = 0.1$, $p_2^1 = 1$, $p_1^2 = 1$, $p_2^2 = 0.1$, $p_1 = 270$, $p_2 = 270$.

The four ecological variables of the continuous trait model are nitrogen concentration (N), total algal density ($A = A_1 + A_2$), and total breeding ($R = R_1 + R_2$) and senescent ($S = S_1 + S_2$) rotifers. The evolutionary variables are $x_1 = A_1/A$, $x_2 = R_1/R$, and $x_3 = S_1/S$. The Jacobian for the continuous trait model is

$$\begin{pmatrix} -0.599 & -223 & 0 & 0 & 8.58 & 0 & 0 \\ 0.000808 & 0.122 & -0.00444 & -0.00444 & -0.00935 & 0 & 0 \\ 0 & 14.4 & 0 & 0 & -1.10 & 0. & 0 \\ 0 & 0 & 0.4 & -0.355 & 0 & 0 & 0 \\ 0.000898 & -0.0685 & 0.0025 & 0.0025 & 0.0816 & 0.116 & 0.131 \\ 0 & -5.74 \cdot 10^{-10} & 0 & 0 & -0.345 & 0. & 0 \\ 0 & 0 & 0. & -2.83 \cdot 10^{-12} & 0 & 0.355 & -0.355 \end{pmatrix} \tag{S.17}$$

where the order of the columns and rows is $(N, A, R, S, x_1, x_2, x_3)$. The ecological subsystem is $\{N, A, R, S\}$ and the complementary evolutionary subsystem is $\{x_1, x_2, x_3\}$. The prey evolutionary subsystem and its complement are $\{x_1\}$ and $\{N, A, R, S, x_2, x_3\}$. The prey eco-evolutionary subsystem and its complement are $\{A, x_1\}$ and $\{N, R, S, x_2, x_3\}$. The predator evolutionary subsystem and its complement are $\{x_2, x_3\}$ and $\{N, A, R, S, x_1\}$. The predator eco-evolutionary subsystem and its complement are $\{R, S, x_2, x_3\}$ and $\{N, A, x_1\}$.

S4.6 Hiltunen et al. (35) Model

The model is

$$
\begin{aligned}
\frac{dS}{dt} &= \delta(1-S) - rS\left(\frac{A_1}{k_1+S} + \frac{A_2}{k_2+S}\right) \\
\frac{dA_i}{dt} &= A_i\left[\frac{rS}{k_i+S} - \frac{p_i g R}{k_R+E_r+\alpha_F F} - \pi_i h F - \delta\right] \\
\frac{dR}{dt} &= R\left[\frac{gE_R}{k_R+E_R+\alpha_F F} + \frac{\eta F}{k_R+E_R+\alpha_F F} - \delta\right] \\
\frac{dF}{dt} &= F\left[hE_F - \frac{\eta R}{k_R+Q+\alpha_F F} - \delta\right] + I_F
\end{aligned}
\tag{S.18}
$$

where S is the concentration of limiting substrate, A_i is the density of algal clones ($i = 1, 2$), R is the density of rotifers (the intraguild predator), and F is the density of flagellates (the intraguild prey). In the model $E_R = p_1A_1 + p_2A_2$ and $E_F = \pi_1A_1 + \pi_2A_2$. The three parameterizations for figures 1b-d are listed below.

The four ecological variables of the continuous trait model are S, $A = A_1 + A_2$, R, and F and the evolutionary variable is $x_1 = A_1/A$. The ecological subsystem is $\{S, A, R, F\}$ and the complementary evolutionary subsystem is $\{x_1\}$; this pair of subsystems also defines the prey evolutionary subsystem and its complement. The prey eco-evolutionary subsystem and its complement are $\{A, x_1\}$ and $\{S, R, F\}$. The predator ecological subsystem and its complement are $\{R, F\}$ and $\{S, A, x_1\}$.

Figure 1b: The parameter values are $\delta = 1$, $r = 2$, $k_1 = 0.234$, $k_2 = 0.19$, $p_1 = 0.05$, $p_2 = 1$, $g = 2$, $k_r = 0.2$, $\alpha_F = 0.05$, $\pi_1 = 1$, $\pi_2 = 0.1$, $h = 3$, $\eta = 0.08$, $I_F = 0.001$. The Jacobian for the continuous trait model is

$$\begin{pmatrix} -1.62 & -1.27 & 0 & 0 & 0.0478 \\ 0.619 & 0.06 & -0.985 & -0.99 & -0.0705 \\ 0 & 0.0604 & 0 & 0.00455 & -0.0715 \\ 0 & 0.144 & -0.0142 & -0.014 & 0.0943 \\ 0.0166 & -0.0664 & 1.1 & -0.635 & 0.0786 \end{pmatrix} \tag{S.19}$$

where the order of the columns and rows is (S, A, R, F, x).

Figure 1c: The parameter values are $\delta = 1$, $r = 3.3$, $k_1 = 0.1475, k_2 = 0.07375$, $p_1 = 0.05$, $p_2 = 1$, $g = 2.5$, $k_R = 0.2$, $\alpha_F = 0.05$, $\pi_1 = 1$, $\pi_2 = 0.05$, $h = 3$, $\eta = 0.4$, $I_F = 0.001$. The Jacobian for the continuous trait model is

$$\begin{pmatrix} -3.19 & -1.83 & 0 & 0 & 0.244 \\ 2.19 & 0.06 & -0.682 & -1.18 & -0.149 \\ 0 & 0.132 & 0 & 0.176 & -0.327 \\ 0 & 0.635 & -0.318 & 0.00367 & 0.231 \\ 0.0824 & -0.081 & 0.928 & -0.347 & 0.202 \end{pmatrix} \tag{S.20}$$

where the order of the columns and rows is (S, A, R, F, x).

Figure 1d: The parameter values are $\delta = 1$, $r = 2$, $k_1 = 0.19$, $k_2 = 0.12$, $p_1 = 0.1$, $p_2 = 1$, $g = 2$, $k_R = 0.2$, $\alpha_F = 0.05$, $\pi_1 = 1$, $\pi_2 = 1$, $h = 3$, $\eta = 0.4$, $I_F = 0.001$. The Jacobian for the continuous trait model is

$$\begin{pmatrix} -1.26 & -1.5 & 0 & 0 & 0.0571 \\ 0.263 & 0.0343 & -0.844 & -1.03 & -0.0241 \\ 0 & 0.0407 & 0 & 0.0323 & -0.0285 \\ 0 & 0.425 & -0.156 & -0.00645 & -0.00445 \\ 0.0419 & -0.0481 & 1.18 & -0.00546 & 0.0337 \end{pmatrix} \tag{S.21}$$

where the order of the columns and rows is (S, A, R, F, x).

S4.7 Kasada et al. (27) Model

The model is

$$\begin{aligned} \frac{dN}{dt} &= \delta(N_I - N) - \frac{\omega_c}{\varepsilon_c} \sum_i \frac{\beta_i N C_i}{K_c + N} \\ \frac{dC_i}{dt} &= C_i \left[\chi_c \frac{\omega_c}{\varepsilon_c} \frac{\beta_i N}{K_c + N} - \frac{G p_i B}{K_b + p_1 C_1 + p_2 C_2} - \delta \right] \\ \frac{dB}{dt} &= B \chi_b \frac{G(p_1 C_1 + p_2 C_2)}{K_b + p_1 C_1 + p_2 C_2} - (m + \delta) B \end{aligned} \tag{S.22}$$

where N is concentration of nitrogen, C_i is the density of algal clones ($i = 1, 2$), and B is the density of rotifers. We only focus on the parameter values for the UTEX396 and UTEX265 algal clones because coexistence of multiple clonal types did not occur for other combinations. This corresponds to figure 4E in Kasada et al. (27). The parameter values are $\beta_1 = 1.77$, $\beta_2 = 1.57$, $p_1 = 0.102$, $p_2 = 0.102 \cdot 0.688$, $N_I = 80$, $\delta = 0.5$, $\chi_c = 0.05$, $\chi_b = 54000$, $m = 0.055$, $K_c = 4.3$, $K_b = 0.835$, $\omega_c = 20$, $\varepsilon = 1$, $G = 5 \cdot 10^{-5}$.

For the continuous trait model the ecological variables are N, $C = C_1 + C_2$, and B and the evolutionary variable is $x_1 = C_1/C$. The Jacobian for the system is

$$\begin{pmatrix} -6.74 & -14.6 & 0 & -4.65 \\ 0.312 & 0.047 & -0.0000103 & 0.00478 \\ 0 & 9822 & 0 & 9980 \\ 0.0034 & 0.0016 & -3.57 \cdot 10^{-7} & 0.00166 \end{pmatrix} \tag{S.23}$$

where the order of the columns and rows is (N, C, B, x). The ecological subsystem is $\{N, C, B\}$ and the complementary evolutionary subsystem is $\{x_1\}$; this pair of subsystems also defines the prey evolutionary subsystem and its complement. The prey eco-evolutionary subsystem and its complement are $\{C, x_1\}$ and $\{N, B\}$. The predator ecological subsystem and its complement are $\{B\}$ and $\{N, C, x_1\}$.

S4.8 Wei et al. (34) Model

The model is

$$
\begin{aligned}
\frac{dR}{dt} &= w(C-R) - \frac{R}{k+R}e(vN + v_1N_1 + v_2N_2 + v_{12}N_{12}) \\
\frac{dN}{dt} &= \psi(R)N - \delta_1(R)NP_1 - \delta_2(R)NP_1 - \frac{R}{R+k}[nxN - xnX] - nwN + wnNW - wN \\
\frac{dN_1}{dt} &= \psi_1(R)N_1 - \delta_1(R)N_1P_1 - \delta_2(R)N_1P_1 - \frac{R}{R+k}[nxN_1 - xnX_1] - nwN_1 + wnNW_1 - wN_1 \\
\frac{dN_2}{dt} &= \psi_2(R)N_2 - \delta_1(R)N_2P_1 - \delta_2(R)N_2P_1 - \frac{R}{R+k}[nxN_2 - xnX_2] - nwN_2 + wnNW_2 - wN_2 \\
\frac{dN_{12}}{dt} &= \psi_{12}(R)N_{!2} - wN_{12} \\
\frac{dNW}{dt} &= nwN - wnNW - wwN \\
\frac{dNW_1}{dt} &= nwN_1 - wnNW_1 - wwN_1 \\
\frac{dNW_2}{dt} &= nwN_2 - wnNW_2 - wwN_2 \\
\frac{dX}{dt} &= \frac{R}{R+k}[nxN - xnX] - wX \\
\frac{dX_1}{dt} &= \frac{R}{R+k}[nxN_1 - xnX_1] - wX_1 \\
\frac{dX_2}{dt} &= \frac{R}{R+k}[nxN_2 - xnX_2] - wX_2 \\
\frac{dP_1}{dt} &= P_1\left[\delta_1(R)(N+N_2)(\beta_1(R)-1))\right] - wP_1 \\
\frac{dP_2}{dt} &= P_2\left[\delta_2(R)(N+N_1)(\beta_2(R)-1))\right] - wP_2
\end{aligned}
\tag{S.24}
$$

where the variables are phage densities (P_1, P_2), planktonic, non-persistor bacteria densities (N, N_1, N_2, N_{12}), persistor bacteria densities (X_1, X_2, X_3) and wall bacteria densities (NW, NW_1, NW_2); the subscripts for the bacteria populations denote which phage the bacteria is resistant to. The functions in the model are

$$
\begin{aligned}
\phi(R) &= \frac{vR}{R-k} \\
\delta_i(R) &= (1-x)\delta_{max,i} + x\delta_{max,i}\frac{R}{R+k} \\
\beta_i(R) &= (1-x)\beta_{max,i} + x\beta_{max,i}\frac{R}{R+k}
\end{aligned}
\tag{S.25}
$$

The parameter values are $v = 1$, $k = 0.25$, $e = 5 \cdot 10^{-7}$, $\delta_{max,1} = 0.1 \cdot 10^{-7}$, $\delta_{max,2} = 0.1 \cdot 10^{8}$, $\beta_{max,1} = 50$, $\beta_{max,2} = 100$, $x = 0.5$, $w = 0.4$, $ww = 0.01$, $C = 100$, $nx = 0.0001$, $xn = 0.0001$, $nw = 0.01$, $wn = 0.005$, $v_1 = 0.9$, $v_2 = 0.85$, $v_{12} = 0.8$.

Figure 5a: This parameterization assumes N, X, NW, and N_{12} are not present, i.e., there are no bacteria susceptible to both or none of the phage types. The ecological variables of the continuous trait model are the total densities of the different bacterial types and phage: $\bar{N} = N_1 + N_2$, $N\bar{W} = NW_1 + NW_2$, $\bar{X} = X_1 + X_2$, and $\bar{P} = P_1 + P_2$. To avoid notational confusion, we use χ_i to denote the evolutionary traits. The evolutionary variables are $\chi_1 = N_1/\bar{N}$, $\chi_2 = NW_2/N\bar{W}$, $\chi_3 = X_1/\bar{X}$, and $\chi_4 = P_1/\bar{P}$. The Jacobian for the system is

$$
\begin{pmatrix}
-0.4 & -4.45 \cdot 10^{-7} & 0 & 0 & 0 & -0.121 & 0 & 0 & 0 \\
88 & -0.00333 & 0.005 & 9.97 \cdot 10^{-5} & -0.00439 & 0 & 0 & 0 & -2.21 \cdot 10^{6} \\
0 & 0.01 & -0.015 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.0135 & 9.97 \cdot 10^{-5} & 0 & -0.4 & 0 & 0 & 0 & 0 & 0 \\
5996 & 44 & 0 & 0 & 0 & 1.31 \cdot 10^{8} & 0 & 0 & 0 \\
9.73 \cdot 10^{-8} & 0 & 0 & 0 & -1.3 \cdot 10^{-11} & -0.00333 & 0.00333 & 2.49 \cdot 10^{-8} & 0.823 \\
0 & 0. & 0 & 0 & 0 & 0.015 & -0.015 & 0 & 0 \\
0 & 0. & 0 & 0 & 0 & 0.4 & 0 & -0.4 & 0 \\
0 & 0 & 0 & 0 & 0 & -0.216 & 0 & 0 & 0
\end{pmatrix}
\tag{S.26}
$$

where the order of the columns and rows is $(R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}, \chi_1, \chi_2, \chi_3, \chi_4)$. The eco-

logical subsystem is $\{R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}\}$ and the complementary evolutionary subsystem is $\{x_1, x_2, x_3, x_4\}$. The prey evolutionary subsystem and its complement are $\{x_1, x_2, x_3\}$ and $\{R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}, x_4\}$. The prey eco-evolutionary subsystem and its complement are $\{\bar{N}, N\bar{W}, \bar{X}, x_1, x_2, x_3\}$ and $\{R, \bar{P}, x_4\}$. The predator evolutionary subsystem and its complement are $\{x_4\}$ and $\{R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}, x_1, x_2, x_3\}$. The predator eco-evolutionary subsystem and its complement are $\{\bar{P}, x_4\}$ and $\{R, \bar{N}, N\bar{W}, \bar{X}, x_1, x_2, x_3\}$.

Figure 5b: This parameterization assumes N_2, X_2 and NW_2 are not present, i.e., there are no types that are just resistant to phage 2. For the continuous trait model the ecological variables are the total densities of the different bacterial types and phage: $\bar{N} = N + N_1 + N_{12}$, $N\bar{W} = NW + NW_1$, $\bar{X} = X + X_1$, and $\bar{P} = P_1 + P_2$. To avoid notational confusion, we use χ_i to denote the evolutionary traits. The evolutionary variables are $\chi_1 = N_1/\bar{N}$, $\chi_2 = N_{12}/\bar{N}$, $\chi_3 = NW/N\bar{W}$, $\chi_4 = X/\bar{X}$, and $\chi_5 = P_1/\bar{P}$. The Jacobian for the system is

$$\begin{pmatrix}
-80.2 & -2.01\cdot 10^{-7} & 0 & 0 & 0 & 4.96 & 9.92 & 0 & 0 & 0 \\
1.59\cdot 10^{8} & -0.000121 & 0.005 & 0.00005 & -0.006 & 0. & 6.61\cdot 10^{5} & 0 & 0 & -3.58\cdot 10^{5} \\
0 & 0.000363 & -0.015 & 0 & 0 & 0 & -1.98\cdot 10^{6} & 0 & 0 & 0 \\
721 & 1.82\cdot 10^{-6} & 0 & -0.4 & 0 & 0 & -9920 & 0 & 0 & 0 \\
3.46\cdot 10^{7} & 0.13 & 0 & 0 & 0 & -3.62\cdot 10^{8} & -9.98\cdot 10^{8} & 0 & 0 & 0 \\
0.00197 & -4.69\cdot 10^{-13} & 1.94\cdot 10^{-11} & 1.94\cdot 10^{-13} & -1.86\cdot 10^{-11} & -0.00333 & -9.65\cdot 10^{-5} & -0.000121 & -2.27\cdot 10^{-10} & 0.00145 \\
-0.00296 & 5.88\cdot 10^{-13} & -2.43\cdot 10^{-11} & -2.43\cdot 10^{-13} & 2.9\cdot 10^{-11} & \cdot 10^{-20} & -0.00321 & 0 & 0 & 0.00174 \\
0 & 0 & 0 & 0 & 0 & -0.413 & -0.33 & -0.015 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & -11 & -8.78 & 0 & -0.4 & 0 \\
0.000344 & 0 & 0 & 0 & 0 & -5.04 & -4.02 & 0 & 0 & 0
\end{pmatrix} \tag{S.27}$$

where the order of the columns and rows is $(R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}, \chi_1, \chi_4, \chi_2, \chi_3, \chi_5)$. The ecological subsystem is $\{R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}\}$ and the complementary evolutionary subsystem is $\{x_1, x_2, x_3, x_4, x_5\}$. The prey evolutionary subsystem and its complement are $\{x_1, x_2, x_3, x_4\}$ and $\{R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}, x_5\}$. The prey eco-evolutionary subsystem and its complement are $\{\bar{N}, N\bar{W}, \bar{X}, x_1, x_2, x_3, x_4\}$ and $\{R, \bar{P}, x_5\}$. The predator evolutionary subsystem and its

complement are $\{x_5\}$ and $\{R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}, x_1, x_2, x_3, x_4\}$. The predator eco-evolutionary subsystem and its complement are $\{\bar{P}, x_5\}$ and $\{R, \bar{N}, N\bar{W}, \bar{X}, x_1, x_2, x_3, x_4\}$.

S4.9 Yoshida et al. (11; 12) Model

The model is

$$\begin{aligned}
\frac{dN}{dt} &= \delta(VN_I - N) - \frac{\omega_c}{\varepsilon_c}\sum_i \frac{\beta_c C_i N/V}{K_{c,i} + N/V} \\
\frac{dC_i}{dt} &= C_i\left[\chi_c \frac{\omega_c}{\varepsilon_c}\frac{\beta_c C_i N/V}{K_{c,i} + N/V} - \frac{G p_i B}{K_b + p_1 C_1 + p_2 C_2} - \delta\right] \\
\frac{dB}{dt} &= R\chi_b \frac{G(p_1 C_1 + p_2 C_2)}{K_b + p_1 C_1 + p_2 C_2} - (m+\delta)B \\
\frac{dR}{dt} &= R\chi_b \frac{G(p_1 C_1 + p_2 C_2)}{K_b + p_1 C_1 + p_2 C_2} - (m+\delta+\lambda)R
\end{aligned} \tag{S.28}$$

where N is concentration of nitrogen, C_i is the density of algal clones ($i = 1, 2$), and B and R are the total rotifer density and density of fertile rotifers, respectively. In the model $K_{c,i} = K_{min} + \alpha_2(1 - p_i^{\alpha_1})^{1/\alpha_2}$. The parameters are $N_I = 80$, $V = 0.33$, $K_{min} = 4.3$, $K_b = 0.292$, $\beta_c = 3.3$, $\alpha_1 = 0.8$, $\alpha_2 = 9.5$, $p_{min} = 0.02$, $\delta = 0.69$, $\chi_b = 5400$, $\chi_c = 0.05$, $\omega_c = 20$, $\varepsilon_c = 1$, $G = 3.3 \cdot 10^{-4}$, $\lambda = 0.4$, $m = 0.055$, $p_1 = 0.02$, $p_2 = 1$.

For the continuous trait model the ecological variables are N, $C = C_1 + C_2$, B, and R and the evolutionary variable is $x_1 = C_1/C$. The Jacobian for the system is

$$\begin{pmatrix}
-18.7 & -16.5 & 0 & 0 & 5.55 \\
0.9 & 0.0877 & -0.000212 & 0 & -0.178 \\
0 & 171 & -0.745 & 1.15 & -349 \\
0 & 171 & 0 & 0 & -349 \\
-0.0443 & -0.0388 & 0.0000939 & 0 & 0.079
\end{pmatrix} \tag{S.29}$$

where the order of the columns and rows is (N, C, B, R, x_1). The ecological subsystem is $\{N, C, B, R\}$ and the complementary evolutionary subsystem is $\{x_1\}$; this pair of subsystems also defines the prey evolutionary subsystem and its complement. The prey eco-evolutionary

subsystem and its complement are $\{C, x_1\}$ and $\{N, B, R\}$. The predator ecological subsystem and its complement are $\{B, R\}$ and $\{N, C, x_1\}$.