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

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ABSTRACT: We develop a novel method to identify how ecological, evolutionary, and eco-evolutionary feedbacks influence system stability. Our method determines how system stability is influenced by the stabilities of a focal subsystem (i.e., the dynamics of a subset of variables of a system), its complementary subsystem, and feedbacks between the two subsystems. We apply our theory to nine empirically-parameterized eco-evolutionary models from the literature. We find that ecological feedbacks and evolutionary and eco-evolutionary feedbacks involving exploiter species (predators or pathogens) are typically stabilizing. In contrast, evolutionary and eco-evolutionary feedbacks involving victim species (prey or hosts) are destabilizing more often than not. We also explore how subsystem stability and the speed of evolution interact to determine system stability. These methods coupled with future empirical work at the eco-evolutionary interface will allow us to determine whether the (de)stabilizing effects we observed are common in ecological communities.

Introduction

Understanding the factors that promote or hinder stability remains a fundamental problem in community ecology. A number of empirical and theoretical studies have demonstrated that feedbacks between ecological and evolutionary processes, called eco-evolutionary feedbacks, can alter community stability (Pimentel et al., 1963; Abrams and Matsuda, 1997b; Becks et al., 2010; Cortez and Ellner, 2010; Schreiber et al., 2011; Vasseur et al., 2011; Patel and Schreiber, 2015; Cortez, 2016). In particular, some experimental systems with demonstrated eco-evolutionary feedbacks between population densities and species traits exhibit stable dynamics (Sanchez and Gore, 2013; Frickel et al., 2016), while others are unstable and exhibit cyclic dynamics (Yoshida et al., 2003, 2007; Becks et al., 2010; Hiltunen et al., 2014b; Haafke et al., 2016). In this work, we aim to identify which particular feedbacks cause some empirical systems to be stable, while others to be unstable.

Generally, it is not well understood which particular feedbacks between population densities (ecological feedbacks), between trait dynamics (evolutionary feedbacks), and between population densities and traits (eco-evolutionary feedbacks) are responsible for driving stable or cyclic population dynamics in empirical systems. Previous theoretical work has explored how ecological, evolutionary and eco-evolutionary feedbacks influence community stability (Cortez, 2016; Patel et al., 2018; Cortez, 2018; Fleischer et al., 2018). From this work, we know that eco-evolutionary feedbacks have the potential to be stabilizing as well as destabilizing, and that their role depends on whether ecological rates of change are faster than evolutionary rates of change, or vice versa.

However, there has been a disconnect between this theory and empirical systems, and 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 there is a separation of time scales between ecology and evolution (i.e., ecological rates of change are either much faster or much slower than rates of evolutionary change). While the predictions from the slow evolution limit are likely to be useful in systems where evolution

is mutation-limited (and therefore slower than ecology), the observed ecological and evolutionary dynamics in the empirical systems cited above suggest that the ecological and evolutionary time scales are commensurate. Thus, current theory is limited in its ability to identify how particular feedbacks influence the stability of population dynamics of empirical systems.

Additionally, many empirical systems involve multiple species interacting and multiple traits evolving. Cortez (2018) showed for a predator-prey system with two species and two traits how one can determine the effect each ecological, evolutionary, and eco-evolutionary feedback has on system stability. However, for larger systems, this approach leads to a combinatorially large number of ecological, evolutionary, and eco-evolutionary feedbacks that could be stabilizing or destabilizing a particular system. Moreover, unless two systems are identical in their composition of types of species and types of traits (e.g., predator-prey system with an evolving prey defense), how to compare effects between systems is unclear. Thus, to identify and compare how different feedbacks determine stability and instability across empirical systems, we need new theoretical tools that identify broadly the effects of all ecological feedbacks, all evolutionary feedbacks, and all eco-evolutionary feedbacks while simultaneously pinpointing the roles of particular feedbacks.

In this study, we develop a new method to identify the effects particular feedbacks have on stability and apply this method to models from the literature that are parameterized to empirical systems. Our method focuses on feedbacks between population densities and evolving population-level traits defined in terms of subsystems (i.e., the dynamics of subsets of species densities and evolving traits). Specifically, we determine how the stability of the whole system is influenced by the stabilities of complementary pairs of subsystems, enabling us to pinpoint the collective and particular effects ecological, evolutionary, and eco-evolutionary feedbacks have on stability.

By applying our method to models parameterized to empirical systems, we identify which specific feedbacks are stabilizing and destabilizing in empirical systems. Across systems, we

find that the evolutionary and eco-evolutionary feedbacks involving exploiters (i.e., predators and pathogens) and ecological feedbacks are generally stabilizing whereas the evolutionary and eco-evolutionary feedbacks involving victims (prey and hosts) can be stabilizing or destabilizing. We also explore how the speed of evolution and subsystem stability interact to determine the stability of the whole system. We find that the stabilities of the ecological subsystems and the evolutionary subsystems predict the stability of whole system when rates of evolution are much slower or faster, respectively, than rates of ecological change. However, in some cases the interactions between subsystems are needed to predict system stability when rates of ecological and evolutionary change are comparable.

Materials and Methods

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 changes in the frequencies of different clonal types (e.g., defended and undefended clones). Three studies (Fussmann et al., 2003; Duffy and Sivars-Becker, 2007; Tuda and Iwasa, 1998) were excluded because the models did not have equilibrium points, a necessary condition to apply our Jacobian-based theory. In total, we identified 9 studies consisting of 6 predator-prey models with either prey evolution or predator-prey coevolution, 1 intraguild predation model with evolution in the basal prey, and 2 host-pathogen models with either host or parasite evolution; 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. (2009) is the only exception because the results are identical for all four model parameterizations.

A general eco-evolutionary model

To explore how ecological, evolutionary, and eco-evolutionary feedbacks influence system stability, we use a general eco-evolutionary community model that encompasses all of the parameterized models that we use 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 population permanence (Patel et al., 2018; Patel and Schreiber, 2018). The model is

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

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

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. The direction of evolution is determined by the sign of the function g_j, with positive values indicating evolution towards larger trait values.

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 $(N = C_1 + C_2)$ and the frequency of clone 1 $(x_1 = C_1/N)$. Similar transformations can be done 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., competition, predation, and mutualism). It is also flexible enough to encompass other bodies of theory used to study eco-evolutionary dynamics, including approaches based on the theory of adaptive dynamics (Marrow et al., 1996; Geritz et al., 1998) and quantitative genetics (Abrams et al., 1993).

Complimentary subsystem pairs method

Our method focuses on how complementary pairs of subsystems of (1) influence the stability of the full system. Here, system stability is defined by the stability of an equilibrium point of model (1), which is determined by the Jacobian (J), i.e., a matrix that determines whether small perturbations from equilibrium decay (implying stability) or grow (implying instability) over time. A subsystem describes the dynamics of a subset of variables when the 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 mutually exclusive sets of variables whose union is all variables in the system). For example, the (n-dimensional) ecological subsystem of a model 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). The complement of the ecological subsystem 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 could be the population and trait dynamics associated with one species, say N_1 and x_1. Then the complementary subsystem would be the population and trait dynamics of the remaining species: $N_2, \ldots, N_n, x_2, \ldots, x_m$.

The stability of the whole system is affected by the stability of its subsystems. The stability of a subsystem is determined by the submatrix made up of the Jacobian entries that only involve the variables of the subsystem (see appendix S1 for details). Specifically,

unstable subsystems have destabilizing effects on the stability of the whole system. Mathematically, unstable subsystems are defined by submatrices that have at least one eigenvalue with positive real part. Stable subsystems (all eigenvalues have negative real part) and neutrally stable subsystems (all eigenvalues have non-zero real parts and at least one has strictly negative real part) have stabilizing effects on the stability of the whole system. Neutral subsystems (all eigenvalues have zero real parts) do not directly effect on the stability of the whole system but can indirectly affect it through their interactions with other subsystems.

When analyzing the parameterized models from the literature, we consider four different pairs of complementary systems, chosen to elucidate the effects of particular biologically-relevant feedbacks. 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 evolutionary variables for 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 all ecological and evolutionary variables 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 (e.g., a subsystem made up of all predator densities and traits) and its complement (figure 1D) to identify how the feedbacks within a particular trophic level influence system stability.

By comparing the stabilities of the full system and a pair of complementary subsystems, we can predict how the feedbacks within and between the complementary subsystems influence the stability of the full system. There are three possibilities. First, if the stability of the whole system differs from the stabilities of both complementary subsystems, then the stability of the whole system is due to interactions between the subsystems. In this case the feedbacks between subsystems are stronger than the feedbacks within subsystems. For ex-

ample, if the whole system is unstable and the n-dimensional ecological and m-dimensional evolutionary subsystems are stable, then instability of the full system is caused by destabilizing eco-evolutionary feedbacks. Similarly, if the whole system is stable and the n-dimensional ecological and m-dimensional evolutionary subsystems are unstable, then stability of the full system is caused by stabilizing eco-evolutionary feedbacks. Second, if the full system is unstable and one or both of the complementary subsystems are unstable, then instability is due to the destabilizing effects of the unstable subsystem(s) and any destabilizing feedbacks between the subsystems. In this case, any stabilizing feedbacks between and within subsystems are weaker than the unstable feedbacks between and within subsystems. For example, if the n-dimensional ecological subsystem is unstable and the m-dimensional evolutionary subsystem is stable, then instability of the full system is caused by destabilizing ecological and eco-evolutionary feedbacks being stronger than stabilizing evolutionary and eco-evolutionary feedbacks. Third, if the full system is stable and one or both of the complementary subsystems are stable, then stability of the full system is due to the stabilizing effects of the stable subsystem(s) and any stabilizing feedbacks between the subsystems. In this case, any stabilizing feedbacks between and within subsystems are stronger than the destabilizing feedbacks between and within subsystems. For example, if the n-dimensional ecological subsystem is unstable and the m-dimensional evolutionary subsystem is stable, then stability of the full system is caused by stabilizing evolutionary and eco-evolutionary feedbacks being stronger than destabilizing ecological and eco-evolutionary feedbacks.

Effects of varied evolutionary speed

Current theory (Cortez, 2016; Cortez and Patel, 2017; Patel et al., 2018; Cortez, 2018) predicts that system stability depends on both the stabilities of subsystems and the speed of evolution relative to ecological rates of change. We use the parameterized models to explore how varying the speed of evolution alters the effects of stabilizing and destabilizing ecological, evolutionary, and eco-evolutionary feedbacks on system stability. Current theory predicts

that if evolution is sufficiently fast or sufficiently slow compared to ecology, then system stability is determined, in part, by the stabilities of the ecological and evolutionary subsystems. Specifically, unstable (stable) evolutionary subsystems suggest instability (stability) in the fast evolution limit and unstable (stable) ecological subsystems suggest instability (stability) in the slow evolution limit. However, current theory also shows that these predictions can be altered depending on the stabilities of eco-evolutionary subsystems (Patel et al., 2018; Cortez, 2018). To vary the speed of evolution in our models, we introduced a multiplicative parameter into the right hand side of equation (2) that allowed us to speed up or slow down the rate of evolution; see appendix S2 for details. We then varied the speed of evolution in the nine parameterized models to assess how the speed 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

Our analysis of the nine parameterized eco-evolutionary models from the literature revealed that subsystem stability differed depending on subsystem type (ecological, evolutionary, or eco-evolutionary) and the trophic level of the species in the subsystem (exploiter versus victim); the effects each system and its complementary subsystem pair have on the stability of the whole system are shown in Table 1. Specifically, we found that ecological subsystems were stable (or neutrally stable) in 8 of 9 systems whereas evolutionary subsystems were stable in only 4 of 9 systems. Exploiter (predator or pathogen) ecological, evolutionary, and eco-evolutionary subsystems were stable or neutral in 7 of 9 systems. In contrast, victim (prey or host) ecological, evolutionary, and eco-evolutionary subsystems were stable in 4 of the 9 systems. Taken together, these patterns suggest that in these nine 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 stabilizing or neutral; and the ecological, evolutionary, and eco-evolutionary feedbacks involving the dynamics of victim species could be stabilizing or destabilizing.

We find similar results when comparing the stabilities of the full systems and the complementary subsystem pairs. For the four systems that exhibit cycles ("unstable" in column 4), the ecological subsystems were stable in 3 of 4 systems and the complementary evolutionary subsystems were unstable in 4 of 4 systems. For example, in the Becks et al. (2010) model, predator and prey densities converge to equilibrium when the prey trait is fixed at its equilibrium density (figure 2B) whereas the prey trait diverges from equilibrium when the prey and predator densities are fixed at their equilibrium values (figure 2C). In addition, the evolutionary and eco-evolutionary subsystems involving the victim species were unstable in 4 of 4 systems and their complementary subsystems were stable in 3 of 4 systems. For example, in the Becks et al. (2010) model, the prey density and trait diverge from equilibrium when predator density and nutrient concentration are fixed at their equilibrium values (figure 2D). In contrast, predator density and nutrient concentration converge to their equilibrium values when the prey density and trait are fixed at their equilibrium values (figure 2C). Finally, the predator evolutionary, evolutionary, eco-evolutionary subsystems were stable or neutral in 3 of 4 studies and their complementary subsystems were stable in 4 of 4 systems. Overall, this suggests that the instability of these four systems was due, at least in part, to unstable evolutionary and eco-evolutionary feedbacks involving the victim species that were stronger than the stabilizing ecological feedbacks involving the exploiter species.

For the five stable systems ("stable" in column 4), all subsystems in the subsystem pairs we considered were stable in 2 of 5 systems (Bolker et al., 2009; Frickel et al., 2016). This suggests that in both of these stable systems, the stabilizing effects of the ecological, evolutionary, and eco-evolutionary feedbacks we considered were stronger than any destabilizing feedbacks defined by the interactions between complementary subsystems. For the other

three stable systems, there was one or more subsystem pair where one of the subsystems was unstable and its complement was stable. This suggests that these systems were stable because the unstable feedbacks present in the unstable subsystems were weaker than the stable feedbacks present in the stable subsystems and any stable feedbacks defined by the interactions between the complementary subsystems. For example, while prey evolutionary and eco-evolutionary feedbacks are destabilizing in Kasada et al. (2014), we predict that the full system was stable because those feedbacks were weaker than the stable ecological feedbacks and other eco-evolutionary feedbacks in the system.

Effects of evolutionary speed on stability

When varying the rates of evolution in the nine parameterized models, we observed four qualitatively different patterns as the speed of evolution increased from very slow to very fast. First, for all systems with stable ecological subsystems and unstable evolutionary 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. (2010) model for varied evolutionary speeds. Second, for the Haafke et al. (2016) study where the evolutionary and ecological subsystems were both unstable (U-U in "Eco & Evo" column of Table 1), the system was unstable for all evolutionary speeds. Third, with the exception of the Duffy et al. (2012) model, for all systems where the evolutionary and ecological subsystems were both stable (S-S in "Eco & Evo" column of Table 1), the system was stable for all evolutionary speeds. Fourth, for the (Duffy et al., 2012) model, the system was stable for very fast and very slow evolutionary speeds and unstable for intermediate evolutionary speeds (figure 3D-F).

For all nine parameterized models, the stabilities of the ecological and evolutionary subsystems accurately predicted the stability of the whole system in the limits where evolution is very fast or very slow. Thus, the stabilities of eco-evolutionary feedbacks were not needed to predict system stability in these limits. However, the predictions for the fast and slow

evolution limits did not accurately predict system stability at intermediate rates of evolution for the Duffy et al. (2012) model. In particular, the ecological and evolutionary subsystems (and all other subsystems we considered) were stable, yet the full system was unstable for intermediate evolutionary rates.

Discussion

In this study, we explored how ecological, evolutionary, and eco-evolutionary feedbacks influenced the stability of a collection of empirical systems. Our approach used pairs of complementary subsystems (i.e., the dynamics of complementary subsets of the ecological and evolutionary variables) to help identify which feedbacks were responsible for stabilizing some empirical systems and destabilizing others.

Our results suggest that ecological, evolutionary, and eco-evolutionary feedbacks have different effects on system stability and that those effects may depend on the species trophic level. Across the nine systems, ecological feedbacks tended to be stabilizing. In contrast, evolutionary feedbacks could be stabilizing or destabilizing, with predator evolutionary feedbacks being stabilizing or neutral across all systems and prey evolutionary feedbacks being evenly split between stabilizing and destabilizing. The observed frequencies of stabilizing and destabilizing prey evolutionary feedbacks are consistent with the roughly equal frequencies of stabilizing and disruptive selection observed in empirical systems (Kingsolver and Diamond, 2011). Prey and predator ecological and eco-evolutionary feedbacks also consistently differed, with predator eco-evolutionary feedbacks being stabilizing or neutral and prey eco-evolutionary feedbacks being destabilizing more often than stabilizing.

Our results also help explain why some eco-evolutionary systems are stable whereas others exhibit cycles. For all unstable systems, our theory predicts that the cyclic dynamics were driven by destabilizing prey evolutionary and eco-evolutionary feedbacks. In contrast, in all but one stable system, those feedbacks had stabilizing effects on system stability. Overall,

this suggests that in these nine empirical systems, the prey evolutionary and eco-evolutionary feedbacks were the primary factors determining whether the whole system was stable or unstable. The one exception is the Kasada et al. (2014) study, where destabilizing effects of the prey evolutionary and eco-evolutionary feedbacks were weaker than the stabilizing effects of the other subsystems, resulting in the whole system being stable. Our results about the destabilizing effects of prey evolutionary and eco-evolutionary feedbacks are consistent with previous theoretical studies that predict prey evolution can have destabilizing effects on systems (Abrams and Matsuda, 1997b; Cortez and Ellner, 2010; Cortez, 2016). While theory predicts predator evolutionary and eco-evolutionary feedbacks can also be destabilizing (Abrams and Matsuda, 1997a; Cortez and Patel, 2017), this was not observed in the four systems with predator evolution; the predator evolutionary and eco-evolutionary subsystems were stable or neutral in all four systems.

One advantage of our theoretical approach is that 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 2010; Becks et al. 2010; Turcotte et al. 2013; Crutsinger et al. 2006). 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 that do not involve that trait. For example, initial standing algal genetic variation was manipulated in Becks et al. (2010). Because the system was stable when algal genetic variation was low and unstable when 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 that do not involve 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. In addition, it may be difficult or infeasible to hold one more densities or traits (nearly) constant in a given empirical system. Nonetheless, for parameterized models, it is straightforward to compute the stabilities of the subsystems. Thus, application of our theory to parameterized models tailored to particular systems allows one to make predictions about how specific feedbacks are influencing community stability and dynamics. 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 highlight the need for additional theory to explain how rates of evolution (relative to ecological rates) influence system stability. Evolutionary speeds are determined, in part, by standing genetic variation, and previous empirical studies have shown that altering the standing genetic variation in a population can change the stability of a system (Becks et al., 2010; Hiltunen and Becks, 2014). Current theory, both general (Patel et al., 2018) and tailored to predator-prey systems (Cortez, 2016; Cortez and Patel, 2017; Cortez, 2018), predicts that system stability in the fast and slow evolution limits can be predicted, in part, by the stabilities of the ecological and evolutionary subsystems. For eight of the nine parameterized model, system stability at all evolutionary speeds are predicted just by the stabilities of the ecological and evolutionary subsystems (figure 3). Thus, for these systems, the stabilities of the eco-evolutionary feedbacks are not needed to make qualitatively correct predictions about how system stability depends on the rate of evolution.

In contrast, for the Duffy et al. (2012) model, the full system is unstable at intermediate

evolutionary speeds even though it is stable in the fast and slow evolution limits (figure 3D-F). Other examples of destabilization at intermediate evolutionary speeds have been observed in eco-evolutionary predator-prey models (Cortez, 2016; Cortez and Patel, 2017; Cortez, 2018). For the predator-prey models, destabilization occurs because smaller subsystems (involving fewer variables) are weakly stable compared to larger subsystems (involving more variables), or vice versa (Cortez, 2018). In effect, subsystems of one size have a small effect on the stability of the whole system, subsystems of a different size have a large effect on the stability of the whole system, and this asymmetry destabilizes the system at intermediate evolutionary speeds. Because there is only one unstable subsystem in the Duffy et al. (2012) model, a similar mechanism may explain the pattern in figure 3D-F. However, for that system and more generally, there is a need for theory that explains how the strengths of different ecological, evolutionary, and eco-evolutionary depend on the speed of evolution (Patel et al., 2018), and how that influences system stability at varied speeds of evolution.

While our approach (based on particular pairs of complementary subsystems) has been fruitful in helping to identify how ecological, evolutionary, and eco-evolutionary feedbacks influence system stability, future theoretical work is needed to fully exploit the subsystem-based approach. First, our approach can be applied to a particular subsystem in order to determine what feedbacks within that subsystem are responsible for its stability. For example, the five systems with an unstable prey eco-evolutionary subsystem also had an unstable prey evolutionary subsystem. Because the prey evolutionary subsystem is a subsystem within the prey eco-evolutionary subsystem, this suggests that the instability of the eco-evolutionary subsystems is due, in part, to the destabilizing effects of the prey evolutionary feedbacks. Those same five systems also had unstable prey ecological subsystems. Thus, instability of the eco-evolutionary subsystems must also be due, in part, to the destabilizing effects of the prey ecological feedbacks. Whether the prey ecological and/or prey eco-evolutionary feedbacks are also destabilizing in the other systems can be determined by applying our method to the prey eco-evolutionary subsystems. Second, our approach can be

extended from pairs of complementary subsystems to triple, quadruples, etc. of complementary subsystems to help disentangle the effects of different feedbacks. Third, the approach can also be extended to consider the stabilities of all subsystems. Such an approach has been useful for studying low-dimensional models of only a few species and a few traits (Cortez, 2018). 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. (2011) model with 10 variables has 1023 subsystems. Thus, new theory is needed to help understand what general rules govern how and when the different ecological, evolutionary, and eco-evolutionary feedbacks influence system stability.

Finally, our approach and any extensions may also be useful in purely ecological contexts for disentangling the effects different variables have on system stability. For example, when applied to food webs, our approach can help identify how dynamics within specific trophic levels or between specific groups of species influence system stability. Similarly, for plant-soil communities, our approach could help understand how within-soil and above-soil communities contribute to stability of the whole system. Our approach can also help disentangle the effects environmental dynamics and species dynamics have on system stability, or disentangle the effects behavioral dynamics and species abundance dynamics have on system stability. In total, this work highlights how subsystem stability can be used to understand and compare the dynamics of empirical systems, and points towards future areas of theoretical research.

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Author Contributions

All authors contributed to developing the ideas for the manuscript. MHC wrote the first version of the manuscript and all authors contributed substantially to editing and revising. All authors contributed to model analyses.

References

Abrams, P. A., and H. Matsuda. 1997a. Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. Evolutionary Ecology 11:1–20.

———. 1997b. Prey adaptation as a cause of predator-prey cycles. Evolution 51:1742–1750.

Abrams, P. A., H. Matsuda, and Y. Harada. 1993. Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. Evolutionary Ecology 7:465–487.

Becks, L., S. P. Ellner, L. E. Jones, and N. G. H. Jr. 2010. Reduction of adaptive genetic diversity radically alters eco-evolutionary community dynamics. Ecology Letters 13:989–997.

Bolker, B. M., A. Nanda, and D. Shah. 2009. Transient virulence of emerging pathogens. Journal of the Royal Society Interface 7:811–822.

Cortez, M. H. 2016. How the magnitude of prey genetic variation alters predator-prey eco-evolutionary dynamics. American Naturalist 188:329–341.

———. 2018. Genetic variation determines which feedbacks drive and alter predator-prey eco-evolutionary cycles. Ecological Monographs 88:353–371.

Cortez, M. H., and S. P. Ellner. 2010. Understanding rapid evolution in predator-prey interactions using the theory of fast-slow dynamical systems. The American Naturalist 176:E109–E127.

Cortez, M. H., and S. Patel. 2017. The effects of predator evolution and genetic variation on predator-prey population-level dynamics. Bulletin of Mathematical Biology 79:1510–1538.

Crutsinger, G. M., M. D. Collins, J. A. Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968.

Duffy, M. A., J. H. Ochs, R. M. Penczykowski, D. J. Civitello, C. A. Klausmeier, and S. R. Hall. 2012. Ecological context influences epidemic size and parasite-driven coevolution. Science 335:1636–1638.

Duffy, M. A., and L. Sivars-Becker. 2007. Rapid evolution and ecological host-parasite dynamics. Ecology Letters 10:44–53.

Fleischer, S. R., C. P. terHorst, and J. Li. 2018. Pick your trade-offs wisely: Predator-prey eco-evo dynamics are qualitatively different under different trade-offs. Journal of Theoretical Biology 456:201–212.

Frickel, J., M. Sieber, and L. Becks. 2016. Eco-evolutionary dynamics in a coevolving host-virus system. Ecology Letters 19:450–459.

Fridley, J. D., and J. P. Grime. 2010. Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. Ecology 91:2272–2283.

Fussmann, G. F., S. P. Ellner, and J. N. G. Hairston. 2003. Evolution as a critical component of plankton dynamics. Proceedings of the Royal Society of London B 270:1015–1022.

Geritz, S. A. H., É. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology 12:35–57.

Haafke, J., M. A. Chakra, and L. Becks. 2016. Eco-evolutionary feedback promotes Red Queen dynamics and selects for sex in predator populations. Evolution 70:641–652.

Hiltunen, T., and L. Becks. 2014. Consumer co-evolution as an important component of the eco-evolutionary feedback. Nature Communications 5:5226.

Hiltunen, T., S. P. Ellner, G. Hooker, L. E. Jones, and N. G. Hairston, Jr. 2014a. Eco-evolutionary dynamics in a three-species food web with intraguild predation: Intriguingly complex. Advances in Ecological Research 150:41–74.

Hiltunen, T., N. G. Hairston, Jr., G. Hooker, L. E. Jones, and S. P. Ellner. 2014b. A newly discovered role of evolution in previously published consumer-resource dynamics. Ecology Letters 17:915–923.

Kasada, M., M. Yamamichi, and T. Yoshida. 2014. Form of an evolutionary tradeoff affects eco-evolutionary dynamics in a predator-prey system. PNAS 111:16035–16040.

Kingsolver, J. G., and S. E. Diamond. 2011. Phenotypic selection in natural populations: what limits directional selection? The American Naturalist 177:346–357.

Marrow, P., U. Dieckmann, and R. Law. 1996. Evolutionary dynamics of predator-prey systems: an ecological perspective. Journal of Mathematical Biology 34:556–578.

Patel, S., M. H. Cortez, and S. J. Schreiber. 2018. Partitioning the effects of ecology, evolution, and eco-evolutionary feedbacks on community stability. American Naturalist 191:381–394.

Patel, S., and S. J. Schreiber. 2015. Evolutionary-driven shifts in communities with intraguild predation. The American Naturalist 186:E98–E110.

———. 2018. Robust permanence for ecological equations with internal and external feedbacks. Journal of mathematical biology 77:79–105.

Pimentel, D., W. Nagel, and J. L. Madden. 1963. Space-time structure of the environment and the survival of parasite-host systems. The American Naturalist 97:141–167.

Sanchez, A., and J. Gore. 2013. Feedback between population and evolutionary dynamics determines the fate of social microbial populations. PLoS Biology 11:e1001547.

Schreiber, S. J., R. Bürger, and D. I. Bolnick. 2011. The community effects of phenotypic and genetic variation within a predator population. Ecology 92:1582–1593.

Tuda, M., and Y. Iwasa. 1998. Evolution of contest competition and its effects on host-parasitoid dynamics. Evolutionary Ecology 12:855–870.

Turcotte, M. M., D. N. Reznick, and J. D. Hare. 2013. The impact of rapid evolution on population dynamics in the wild: experimental test of eco-evolutionary dynamics. Ecology Letters 14:1084–1092.

Vasseur, D. A., P. Amarasekare, V. H. W. Rudolf, and J. M. Levine. 2011. Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. American Naturalist 178:E96–E109.

Wei, Y., A. Kirby, and B. R. Levin. 2011. The population and evolutionary dynamics of *Vibrio cholerae* and its bacteriophage: conditions for maintaining phage-limited communities. The American Naturalist 178:715–728.

Yoshida, T., S. P. Ellner, L. E. Jones, B. J. M. Bohannan, R. E. Lenski, and N. G. Hairston, Jr. 2007. Cryptic population dynamics: rapid evolution masks trophic interactions. PLoS Biology 5:1–12.

Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and N. G. Hairston, Jr. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. Nature 424:303–306.

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. (2010)	Prey	Unstable	S - U	U - S	U - S		S - U
Frickel et al. (2016)	Both	Stable	S - S	S - S	S - S	S - S	S - S
Haafke et al. (2016)	Both	Unstable	U - U	U - U	U - S	S - U	S - U
Kasada et al. (2014)	Prey	Stable	S - U	U - S	U - S		N - U
Wei et al. (2011) 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. (2007, 2003)	Prey	Unstable	S - U	U - S	U - S		N - U
Intraguild predation							
Hiltunen et al. (2014a)‡ 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. (2009)	Parasite	Stable	S - S		S - S	S - S	S - S
Duffy et al. (2012)	Host	Stable	S - S	S - S	S - S		U - S

* The first and second letters describe the effects the subsystem listed in the column and its complementary subsystem,

respectively, have on the stability of the whole system (S= stabilizing effect, U = destabilizing effect, N = neutral effect). 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.

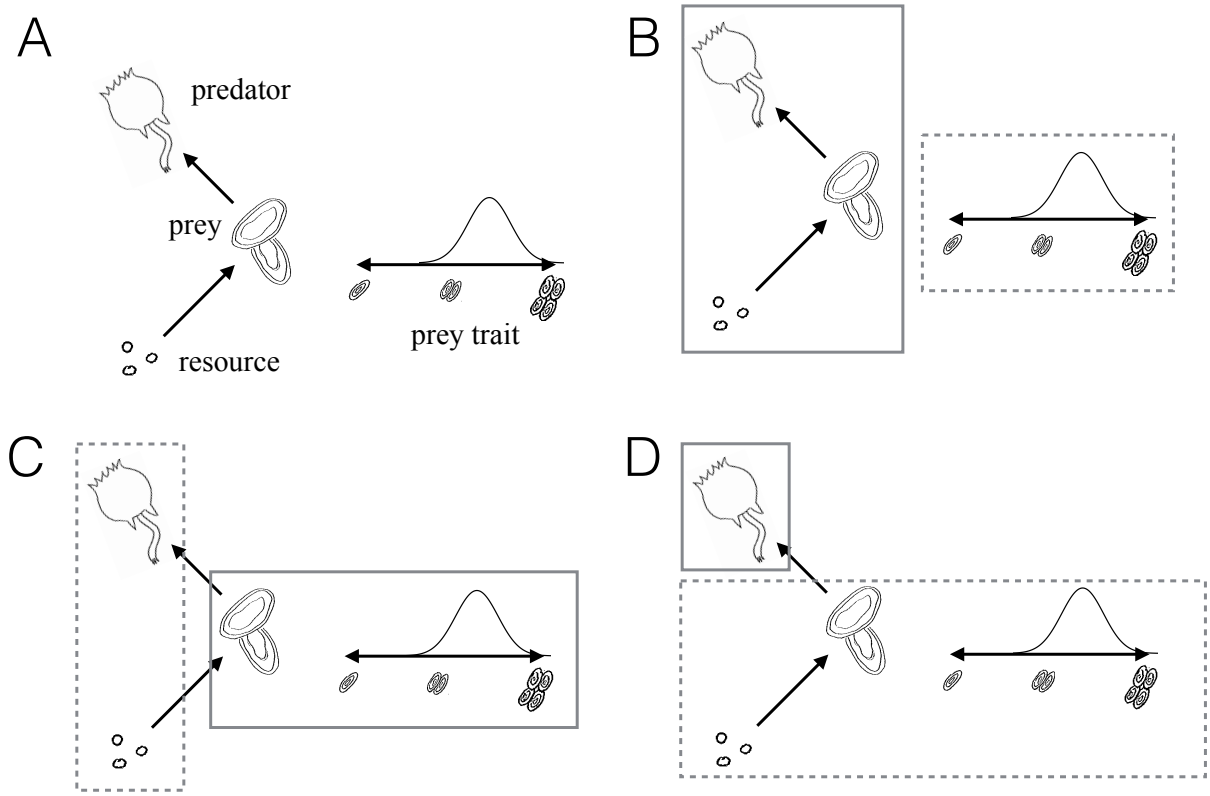

Figure 1: Examples of complementary subsystem pairs in the resource-prey-predator system with an evolving prey trait from Becks et al. (2010). (A) The system dynamics involve changes in resource (nitrogen), prey (algae), and predator (rotifers) densities and the mean clump size of the prey. (B) Ecological 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).

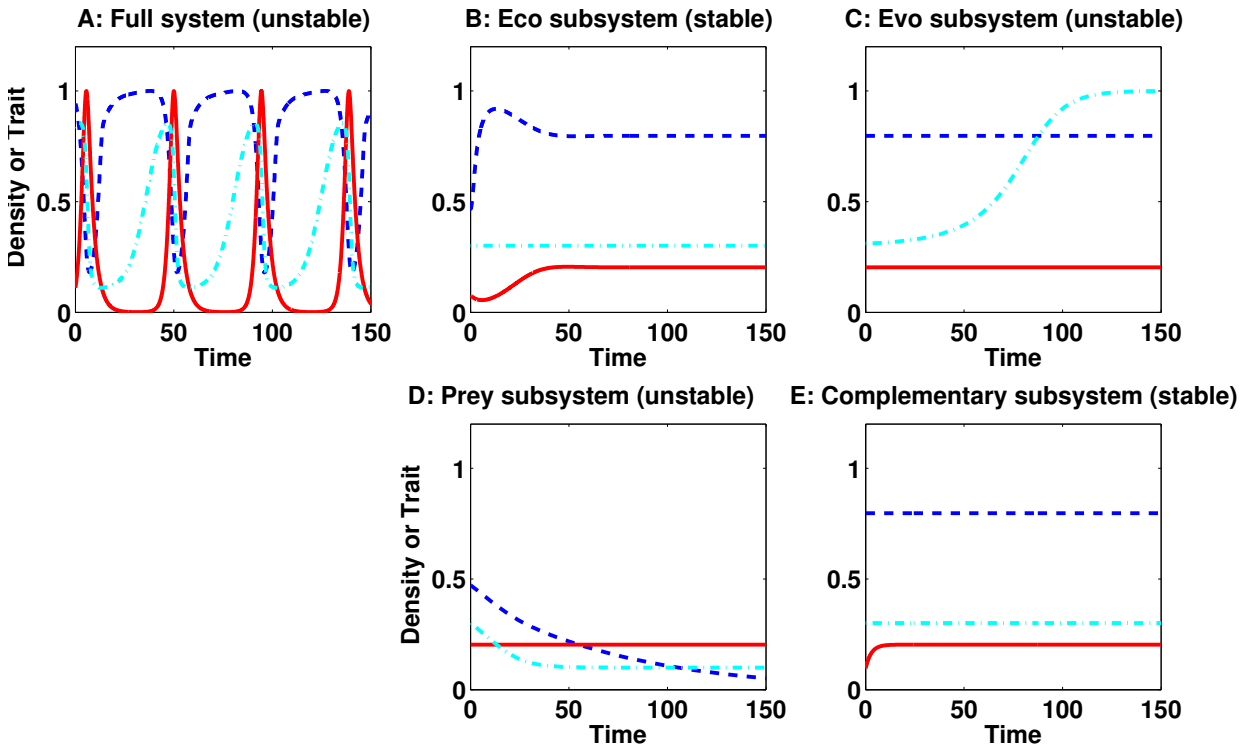

Figure 2: Dynamics and stabilities of the subsystems of the eco-evolutionary predator-prey model in Becks et al. (2010). All panels show scaled prey (dashed blue) and predator (solid red) densities and the proportion of defended prey (dash dot cyan); nutrient dynamics are not shown. (A) The equilibrium of the full 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.

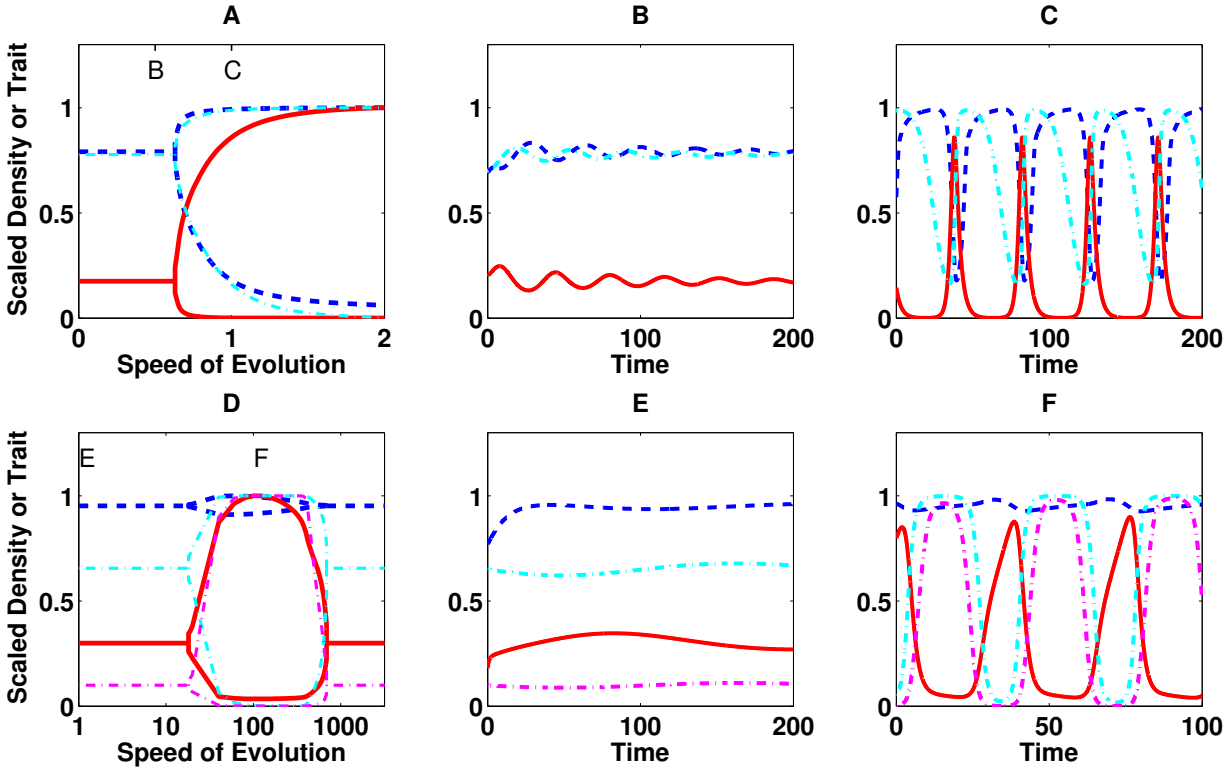

Figure 3: Predicted stability and dynamics of eco-evolutionary models with increased or decreased rates of evolution. (A-C) Dynamics of the Becks et al. (2010) model with prey density (dashed blue), predator density (solid red), and proportion of defended prey (dash-dot cyan). (D-F) Dynamics of the Duffy et al. (2012) 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 the cycle. Letters denote evolutionary speeds for other panels, where a value of one denotes the speed of evolution for the estimated parameter values in the original study.

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 model (1), i.e., an equilibrium where all species have nonzero densities. When evaluated at ρ, the Jacobian of model (1) has the form

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

Note that the diagonal entries for the first n rows have been simplified using $f_i(\rho) = 0$. The full system is stable if all eigenvalues of J have negative real parts, neutrally stable if at least one eigenvalue has zero real part and at least one eigenvalue has negative real part, neutral if all eigenvalues have zero real part, 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. The idea behind our complementary subsystem approach is similar to how the stabilities of one-dimensional subsystems influence the stability of a two-dimensional system. 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 $J_{11} < 0$ ($J_{11} > 0$), the ecological subsystem has a stabilizing (destabilizing) effect on the stability of the whole system. Similarly, when $J_{22} < 0$ ($J_{22} > 0$), the evolutionary subsystem has a stabilizing (destabilizing) effect on the stability of the whole system. Finally, the interactions between the two subsystems have stabilizing (destabilizing) effects when $J_{12}J_{21} > 0$ ($J_{12}J_{21} < 0$). We apply a similar idea to higher dimensional models, where the entries J_{11} and J_{22} are replaced by submatrices of the Jacobian corresponding to a pair of complementary subsystems. Thus, stability of the whole system is affected by the stability of each subsystem as well as the feedbacks between the subsystems. It is important to note that 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.

Another way to see how stable, neutrally stable, unstable, and neutral subsystems influence system stability is to 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.

If the ecological subsystem is stable, then $b_i > 0$ for all i. Because the positive b_i coefficients cause the a_i coefficients to be more positive, the stable ecological subsystem has a stabilizing effect on the stability of the whole system. If the ecological subsystem is neutrally stable, then $b_i \geq 0$ for all i, with at least one of the b_i coefficients being positive. Because the b_i coefficients cause at least one of the a_i coefficients to be more positive and do not cause any of the a_i coefficients to be more negative, the neutrally stable ecological subsystem has a stabilizing effect on the stability of the whole system. If the ecological subsystem is unstable, then one of the b_i coefficients is negative. Because this makes one of the a_i more negative (or equivalently less positive), the unstable ecological subsystems has a destabilizing effect on the stability of the whole system. Finally, if the ecological subsystem is neutral, then $b_i \geq 0$ for all i. If the subsystem has only zero eigenvalues then $b_i = 0$ for all i, the terms in the b_i coefficients have no effect on a_i coefficients, and the neutral subsystem has no direct effect on the stability of the whole system. On the other hand, if the subsystem has purely complex eigenvalues then some b_i coefficients will be positive. Because the b_i coefficients cause at least one of the a_i coefficients to be more positive and do not cause any of the a_i coefficients to be more negative, the neutral ecological subsystem has a stabilizing effect on the stability of the whole system. Note that 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. It is worth noting that the above only focuses on the necessary condition for (sub)system stability, i.e., all coefficients of the characteristic polynomial are negative. 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). Note that 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. Note that 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. Also note that for all models we considered, equilibria can only undergo Hopf bifurcations as the ϵ_i parameters are varied (Patel et al., 2018). Hence, 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 Jacobian and the stabilities of the subsystems for each model can also be reproduced using the accompanying R files. It is important to note that 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. (2010)	Prey	Unstable	S - U	U - S	U - NS		NS - U
Frickel et al. (2016)	Both	Stable	S - S	S - S	NS - NS	S - S	NS - S
Haafke et al. (2016)	Both	Unstable	U - U	U - U	U - NS	NS - U	NS - U
Kasada et al. (2014)	Prey	Stable	S - U	U - S	U - NS		N - U
Wei et al. (2011) 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. (2007, 2003)	Prey	Unstable	S - U	U - S	U - NS		N - U
Intraguild predation							
Hiltunen et al. (2014a)‡ 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. (2009)	Parasite	Stable	S - S		S - NS	S - S	NS - S
Duffy et al. (2012)	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. (2010) 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. (2009) 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. (2012) 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 $x_1 = S_1/S$ 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. (2016) 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. (2016) 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 ($i = 1, 2$), B_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 $(N, A, B, S, x_1, x_2, x_3)$. 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. (2014a) 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. (2014) 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. (2014). 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. (2011) 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. (2003, 2007) 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 $\{N, C, x_1\}$.