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Author for correspondence:
Michael H. Cortez
e-mail: cortez@bio.fsu.edu

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

Michael H. Cortez[1,2], Swati Patel[3] and Sebastian J. Schreiber[4]

[1]Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA
[2]Department of Mathematics and Statistics and Ecology Center, Utah State University, Logan UT 84322, USA
[3]Department of Mathematics, Tulane University, New Orleans, LA 70115, USA
[4]Department of Evolution and Ecology and Center for Population Biology, University of California, Davis, CA 95616, USA

MHC, 0000-0003-2555-7684

We develop a method to identify how ecological, evolutionary, and eco-evolutionary feedbacks influence system stability. We apply our method to nine empirically parametrized eco-evolutionary models of exploiter–victim systems from the literature and identify which particular feedbacks cause some systems to converge to a steady state or to exhibit sustained oscillations. We find that ecological feedbacks involving the interactions between all species and evolutionary and eco-evolutionary feedbacks involving only the interactions between exploiter species (predators or pathogens) are typically stabilizing. In contrast, evolutionary and eco-evolutionary feedbacks involving the interactions between victim species (prey or hosts) are destabilizing more often than not. We also find that while eco-evolutionary feedbacks rarely altered system stability from what would be predicted from just ecological and evolutionary feedbacks, eco-evolutionary feedbacks have the potential to alter system stability at faster or slower speeds of evolution. 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.

1. Introduction

A fundamental problem in community ecology is understanding what factors influence system stability, e.g. whether a community converges to a steady state or exhibits cycles. Empirical and theoretical studies have shown that feedbacks between ecological and evolutionary processes, called eco-evolutionary feedbacks, can influence community stability and lead to different population-level dynamics [1–7]. For example, experimental bacteria and virus-bacteria systems with demonstrated eco-evolutionary feedbacks converge to steady state [8,9], whereas experimental rotifer-algae systems exhibit cycles [3,10–13].

Previous theoretical work has explored the (de)stabilizing effects ecological and evolutionary dynamics have on each other via eco-evolutionary feedbacks. In particular, ecological dynamics have the potential to stabilize unstable evolutionary dynamics or destabilize stable evolutionary dynamics [2,14,15]. Similarly, evolutionary dynamics can stabilize or destabilize ecological dynamics [4,5,15]. In general, stability of a whole system is influenced by the effects species' densities have on the dynamics of population densities (ecological feedbacks), the effects species' traits have on the dynamics of evolving traits (evolutionary feedbacks), and the effects population densities and evolving traits have on each other's dynamics (eco-evolutionary feedbacks). Previous theoretical work [7,15–17] has explored when these feedbacks have stabilizing versus destabilizing effects, and shown that the strengths of those effects increase or decrease with changes in the relative rates of ecological and evolutionary change. Specifically, the stability of the whole system in the slow evolution limit is determined by ecological and eco-evolutionary feedbacks, whereas stability of the whole system in

Table 1. Effects of complementary pairs of subsystems on system stability in parametrized models from the literature.

			stabilities of complementary subsystem pairs[a]				
study	evolving species	system behaviour	eco and evo	victim evo	victim eco or eco-evo[b]	exploiter evo	exploiter eco or eco-evo[b]
predator–prey							
Becks *et al.* [3]	prey	cyclic	S–U	U–S	U–S		S–U
Frickel *et al.* [9]	both	stable	S–S	S–S	S–S	S–S	S–S
Haafke *et al.* [13]	both	cyclic	U–U	U–U	U–S	S–U	S–U
Kasada *et al.* [21]	prey	stable	S–U	U–S	U–S		N–U
Wei *et al.* [22] figure 5a	both	stable	S–S	S–S	S–S	N–S	N–S
figure 5b	both	stable	S–S	S–U	U–S	N–S	N–U
Yoshida *et al.* [10,11]	prey	cyclic	S–U	U–S	U–S		S–U
intraguild predation							
Hiltunen *et al.* [23][c] figure 2.1b	basal prey	cyclic	S–U	U–S	U–S		S–U
figure 2.1c	basal prey	cyclic	S–U	U–S	U–U		U–U
figure 2.1d	basal prey	cyclic	S–U	U–S	U–S		S–U
host-parasite							
Bolker *et al.* [24]	parasite	stable	S–S		S–S	S–S	S–S
Duffy *et al.* [25]	host	stable	S–S	S–S	S–S		U–S

[a] 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).

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

[c] Victim subsystems only involve the basal prey variables and exploiter subsystems involve the intraguild prey and intraguild predator variables.

the fast evolution limit is determined by evolutionary and eco-evolutionary feedbacks.

While these theoretical results identify many possible outcomes, it is not well understood which particular feedbacks are responsible for causing stable versus cyclic population dynamics in empirical systems. First, while the observed rates of ecological and evolutionary change are similar in the above empirical studies, most of the theory assumes ecological rates of change are either much faster or much slower than rates of evolutionary change. Second, because most systems are not identical in their composition of species and traits, it is unclear how to make comparisons across systems. Third, many empirical systems involve multiple interacting species and multiple evolving traits, but because much of the theory focuses on models with a small number of species and traits, it is difficult to apply the theory. Thus, we need new theoretical tools that can extend current theory and identify broadly the effects of ecological, evolutionary, and eco-evolutionary feedbacks while simultaneously pinpointing the importance of particular feedbacks.

Building on prior theoretical work [7,15,16], we develop a method using feedbacks defined in terms of the stability of a subsystem, i.e. the interactions and dynamics of a set of variables when all other variables are held fixed (e.g. the ecological subsystem defines the dynamics of all population densities when all population-level traits are held fixed). Our method identifies how the stabilities of complementary pairs of subsystems (e.g. ecological versus evolutionary subsystems) at the equilibrium of the whole system and the interactions between them (e.g. the effects the evolutionary subsystem has on the ecological subsystem) influence the stability of the whole system. In addition to facilitating comparisons across systems, our method extends the existing theory to systems with any number of species and evolving traits. We apply the method to nine models from the literature that are parametrized to empirical systems. We use the method to identify (i) the effects particular ecological, evolutionary, and eco-evolutionary feedbacks have on stability of the whole system, (ii) when eco-evolutionary feedbacks alter what one would predict about system stability from just ecological and evolutionary feedbacks, and (iii) how those effects are influenced by the relative speeds of ecology and evolution. Our results help explain why some systems exhibit periodic cycles while others converge to steady state.

2. Methods

(a) Selecting parametrized eco-evolutionary models from published studies

To identify studies with parametrized eco-evolutionary models, we searched in 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 parametrized 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 [18–20] were excluded because the models did not have coexistence equilibria with standing genetic variation in at least one population. In total, we identified nine studies consisting of six predator–prey models, one intraguild predation model, and two host-pathogen models; see table 1 for a summary. Multiple entries are listed in table 1 for models with multiple parametrizations; Bolker *et al.* [24] is an exception because the results are identical for all four parametrizations. These nine studies represent all published studies known to the authors.

(b) Method overview

Details about our method are given below and in the electronic supplementary material, appendices S1–S3. In short, we converted each model into a general form, computed the Jacobian and evaluated it at the coexistence equilibrium point determined by the parameters in the original study. With the Jacobian, we determined the stabilities of the various subsystems, compared them to the stability of the whole system, and explored how our results depended on the speed of evolution.

(c) A general eco-evolutionary model

We converted all models into a general form that describes the changes in the densities of n species ($N_1, \ldots, N_n$) and m population-level traits ($x_1, \ldots, x_m$),

$$\left.\begin{array}{ll} & \dfrac{\mathrm{d}N_i}{\mathrm{d}t} = f_i(N_1, \ldots, N_n, x_1, \ldots, x_m), \;\; 1 \le i \le n \\ \text{and} & \dfrac{\mathrm{d}x_j}{\mathrm{d}t} = g_j(N_1, \ldots, N_n, x_1, \ldots, x_m), \;\; 1 \le j \le m. \end{array}\right\} \qquad (2.1)$$

Here, f_i defines the ecological dynamics of species i; it accounts for all (possibly trait-dependent) intra- and interspecific interactions involving species i (e.g. cooperation, competition, predation, and mutualism). The functions g_j define the evolutionary dynamics for each trait, which in general are density and frequency dependent. Note that 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 ($x_1 = C_1/N_1$); see electronic supplementary material, appendix S2 for additional details. Model (2.1) has been used previously to study equilibrium stability and species coexistence [15,26]. It encompasses other bodies of eco-evolutionary theory based on adaptive dynamics [27,28] and quantitative genetics [29].

(d) Complimentary subsystem pairs and subsystem stability

We assume model (2.1) has a unique coexistence equilibrium where all species have positive densities; electronic supplementary material, appendix S1 explains what changes when this assumption is not satisfied. We define stability of the whole system by the stability of the coexistence equilibrium, which 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, for stable systems, all eigenvalues of the Jacobian have negative real parts and for unstable systems, the Jacobian has at least one eigenvalue with a positive real part. Importantly, each empirically parametrized model we considered has a unique coexistence equilibrium and if the coexistence equilibrium is unstable, then the system exhibits cycles because the equilibrium underwent a Hopf bifurcation.

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. For example, the (n-dimensional) ecological subsystem describes the population dynamics of all species ($\mathrm{d}N_i/\mathrm{d}t$ equations) when all traits are fixed at their equilibrium values (solid box in figure 1*b*). Its complement is the (m-dimensional) evolutionary subsystem (dashed box in figure 1*b*), which describes the evolutionary dynamics of all traits ($\mathrm{d}x_j/\mathrm{d}t$ equations) when all population densities are fixed at their equilibrium values. Alternatively, an eco-evolutionary subsystem (solid box in figure 1*c*) could be the population and trait dynamics associated with one species, say N_1 and x_1. Its complementary subsystem (dashed box in figure 1*c*) 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 describing the dynamics of nutrient (N_1), prey (N_2), and predator (N_3) densities and the mean prey trait (x_1); this system is illustrated in figure 1. The Jacobian for this system has the form

$$J = \begin{array}{c|c} \text{Ecological Subsystem} & \text{Effects of Evo on Eco} \\ \left[\begin{array}{ccc} \dfrac{\partial}{\partial N_1}\dfrac{dN_1}{dt} & \dfrac{\partial}{\partial N_2}\dfrac{dN_1}{dt} & \dfrac{\partial}{\partial N_3}\dfrac{dN_1}{dt} \\ \dfrac{\partial}{\partial N_1}\dfrac{dN_2}{dt} & \dfrac{\partial}{\partial N_2}\dfrac{dN_2}{dt} & \dfrac{\partial}{\partial N_3}\dfrac{dN_2}{dt} \\ \dfrac{\partial}{\partial N_1}\dfrac{dN_3}{dt} & \dfrac{\partial}{\partial N_2}\dfrac{dN_3}{dt} & \dfrac{\partial}{\partial N_3}\dfrac{dN_3}{dt} \end{array}\right. & \left.\begin{array}{c} \dfrac{\partial}{\partial x_1}\dfrac{dN_1}{dt} \\ \dfrac{\partial}{\partial x_1}\dfrac{dN_2}{dt} \\ \dfrac{\partial}{\partial x_1}\dfrac{dN_3}{dt} \end{array}\right] \\ \hline \left[\begin{array}{ccc} \dfrac{\partial}{\partial N_1}\dfrac{dx_1}{dt} & \dfrac{\partial}{\partial N_2}\dfrac{dx_1}{dt} & \dfrac{\partial}{\partial N_3}\dfrac{dx_1}{dt} \end{array}\right. & \left.\begin{array}{c} \dfrac{\partial}{\partial x_1}\dfrac{dx_1}{dt} \end{array}\right] \\ \text{Effects of Eco on Evo} & \text{Evolutionary Subsystem} \end{array} \qquad (2.2)$$

The top left box of the Jacobian determines the stability of the ecological subsystem (solid box in figure 1*b*), the bottom right box of the Jacobian determines the stability of the evolutionary subsystem (dashed box in figure 1*b*), and the off-diagonal boxes of the Jacobian determine the effects of ecology on evolution (bottom left) and the effects of evolution on ecology (top right). 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, at least one eigenvalue with strictly negative real part, and at least one eigenvalue with zero real part; and a subsystem is neutral if its submatrix has all eigenvalues with zero real parts; see electronic supplementary material, figure S1 for illustrations of each type of stability.

(e) Stabilities of systems and their complimentary subsystem pairs

When there are no feedbacks between a pair of complementary subsystems, the stability of the whole system is determined by the stabilities of the complementary subsystems: the whole system is stable if both subsystems are stable and the whole system is unstable (implying cycles in our models) if either subsystem is unstable. When there are feedbacks between a pair of complementary subsystems, each subsystem has a stabilizing or destabilizing effect on the stability of the 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 matrix (2.2), then the whole system is predicted to be unstable 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 stabilizing, the whole system can become

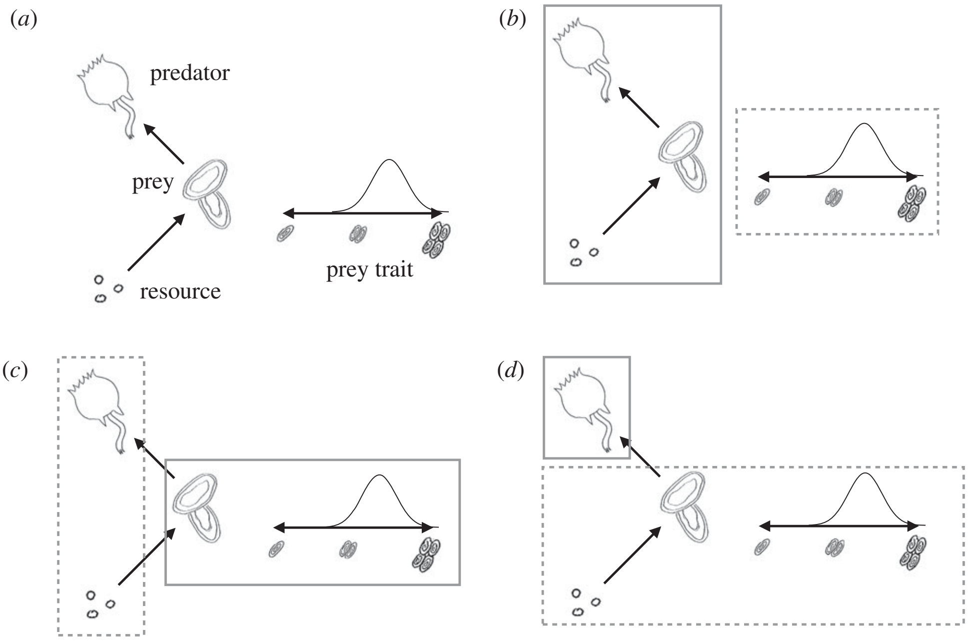

Figure 1. Examples of complementary subsystem pairs in the resource–prey–predator system with an evolving prey trait from Becks *et al.* [3]. (*a*) The system dynamics involve changes in resource (nitrogen), prey (algae), and predator (rotifers) densities and the mean clump size of the prey. (*b*) Ecological 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).

stable. In this case, the feedbacks between the subsystems stabilize the whole system.

We consider four pairs of complementary systems chosen for their biological relevance. First, the complementary ecological and evolutionary subsystems (figure 1*b*) identify the effects of ecological, evolutionary, and eco-evolutionary feedbacks involving all species. Second, the evolutionary subsystem for a single species (i.e. the subsystem composed of all evolving traits of one species) and its complement (also figure 1*b*) identify the effects of evolutionary feedbacks of a single species. Third, 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 1*c*) identify the effects of feedbacks within a single species. Fourth, the subsystem defined by all species and traits in a particular trophic level and its complement (figure 1*d*) identify the effects of feedbacks within a particular trophic level.

We use the stabilities of the complementary subsystem pairs to predict whether different feedbacks have stabilizing or destabilizing effects on the stability of the whole system in two ways. First, the stabilities of the complementary pairs of subsystems identify how subsystems affect the stability of the whole system. Specifically, unstable subsystems have destabilizing effects, stable or neutrally stable subsystems have stabilizing effects, and neutral subsystems have no direct effects on stability (but can indirectly affect stability through their interactions with other subsystems). See the electronic supplementary material, appendix S1 for mathematical details and justifications.

Second, 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 alter the stability of the whole system from what would be predicted from just the stabilities of the complementary subsystems. First, if both subsystems are stable but the whole system is cyclic, then the feedbacks between the subsystems are destabilizing as they are sufficiently strong to counteract the stabilizing effects of the subsystems. 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. 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. Fourth, if one or both subsystems are unstable and the whole system is cyclic, then the feedbacks between the subsystems do not alter the stability of the system.

(f) Effects of varied evolutionary speed

To explore how the interactions between subsystem stability and the speed of evolution influence the stability of the whole system, we varied the speed of evolution in the nine parametrized models. This was done by introducing multiplicative parameters into the right-hand sides of the trait equations in model (2.1); see electronic supplementary material, appendix S3 for details. We then assessed how speeding up and slowing down the rates of evolution influenced system stability and whether stable versus cyclic dynamics in the whole system could be accurately predicted from just the stabilities of the ecological and evolutionary subsystems.

3. Results

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

Across the nine parametrized models from the literature, subsystem stability differed depending on subsystem type (ecological, evolutionary, or eco-evolutionary) and species trophic level (exploiter versus victim; table 1). Specifically, ecological subsystems were stable (or neutrally stable) in eight of the nine systems, whereas evolutionary subsystems were stable in only four systems. Exploiter ecological, evolutionary, and eco-evolutionary subsystems were stable or neutral in seven systems. In contrast, victim ecological, evolutionary, and eco-evolutionary subsystems were stable in four systems.

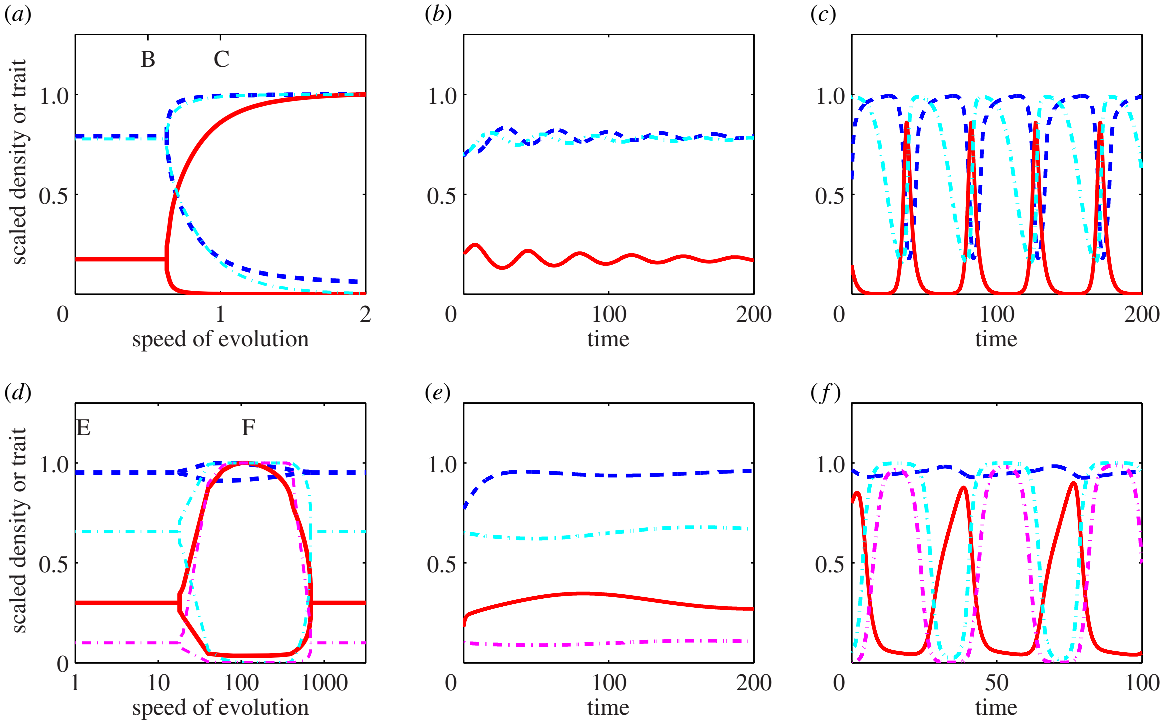

Figure 2. Predicted stability and dynamics of eco-evolutionary models with increased or decreased rates of evolution. (*a–c*) Dynamics of the Becks *et al.* [3] model with prey density (dashed blue), predator density (solid red), and proportion of defended prey (dash-dot cyan); nutrient dynamics are not shown. (*d–f*) Dynamics of the Duffy *et al.* [25] 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. (Online version in colour.)

With this information, we explored if feedbacks between subsystems altered the stability of the whole system from what would be predicted from just the stabilities of complementary subsystem pairs. What role do the feedbacks between subsystems play in influencing the stability of the four empirical systems that exhibit cycles ('cyclic' 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 systems. 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 systems. 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 subsystems play in influencing the stability of the five empirical systems that converge to equilibrium ('stable' in column 4 of table 1)? First, in two systems, all subsystems we considered were stable [9,24]. This means that all feedbacks between the subsystems were either stabilizing or insufficiently strong to destabilize the whole system. Second, in three systems, there was at least one complementary subsystem pair made up of one stable and one unstable subsystem. For each of those 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 subsystems were unstable in Kasada *et al.* [21], the whole system was stable because of the feedbacks between those subsystems and their complements were strongly stabilizing.

(b) Effects of evolutionary speed on stability

We explored how varying the speed of evolution affected system stability in the nine parametrized models. If varying the speed of evolution causes a change in stability, then it either causes a system undergoing cycles to converge to equilibrium or it causes a stable system to exhibit cycles; see electronic supplementary material, appendix S3 for mathematical details. Varying the speed of evolution in the nine parametrized models produced one of four patterns (two shown in figure 2).

First, for the four systems with stable ecological subsystems and unstable evolutionary subsystems (S–U in 'eco and evo' column of table 1), the stability of the whole system switched from stable to unstable as the speed of evolution increased (figure 2*a–c*). In these systems, 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.* [13] study where the ecological and evolutionary subsystems were both unstable, the whole system exhibited cycles for all evolutionary speeds. 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 and evo' column of table 1), the whole 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, the Duffy *et al.* [25] system, where the ecological and evolutionary subsystems were both stable, the whole system was stable for very fast and very slow evolutionary speeds and unstable for intermediate evolutionary speeds (figure 2*d–f*). 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 only for intermediate speeds of evolution. A similar pattern has been observed in eco-evolutionary predator–prey models [7,16,30], but it is unclear if the same mechanisms are driving the pattern in the Duffy *et al.* [25] model because we lack general theory on when and why destabilization occurs at intermediate rates of evolution.

Overall, we found that the feedbacks between the ecological and evolutionary subsystems could alter the stability of the system at some evolutionary speed in five of the nine systems.

4. Discussion

Our results identified that ecological, evolutionary, and eco-evolutionary feedbacks have systematically different effects on the stabilities of empirical systems and that those effects can depend on the species trophic level. Across the nine empirically parametrized models, ecological feedbacks tended to be stabilizing. In contrast, exploiter evolutionary feedbacks were stabilizing or neutral and victim evolutionary feedbacks were 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 parametrized 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 sustained cycles. (Recall that for our nine parametrized models, instability of the coexistence equilibrium implies cyclic dynamics.) The evolutionary subsystems were unstable in the four systems exhibiting cycles and stable in four of the five stable systems. This suggests that evolutionary feedbacks were important drivers of the stability of our nine systems. In addition, in our models, instability and stability of evolutionary subsystems correspond to the disruptive and stabilizing selection, respectively [2]. Stabilizing and disruptive selection are observed with roughly equal frequencies across a broad set of empirical systems [30], suggesting 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, implying eco-evolutionary feedbacks between all species did not alter the stability of the whole system. The one exception is the Kasada *et al.* [21] study, where we predict the eco-evolutionary feedbacks stabilized the whole system. Second, 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, the eco-evolutionary feedbacks between the densities and traits of victim species could be stabilizing or destabilizing. This is consistent with prior theory predicting prey eco-evolutionary feedbacks can be stabilizing or destabilizing [2,4,7]. By contrast, we found that the eco-evolutionary feedbacks between the densities and traits of exploiter species were stabilizing. Current theory predicts predator eco-evolutionary feedbacks can also be destabilizing [31,32], but 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 [3,33–35]. 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. Similarly, holding a species' density nearly fixed will yield information about the stabilities of subsystems without that species. However, in most cases, subsystem stability cannot be determined by experiments where a variable is removed or changed substantially from its equilibrium value (e.g. removing a predator). This is because our subsystem-based approach 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 tailored, parametrized models 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 the relative rates of evolution and ecology influence system stability. First, following Cortez [16], our approach can be extended to consider the effects of all subsystems. However, in systems with many species, the number of subsystems becomes very large, e.g. the Wei *et al.* [22] 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. Second, while current theory [7,15,16,32] can explain model stability in the fast and slow evolution limits, we have a limited ability to make predictions about system stability when rates of ecology and evolution are similar. For example, it is unclear why the Duffy *et al.* [25] model exhibits cycles only at intermediate evolutionary speeds (figure 2*d–f*). This pattern has been observed in eco-evolutionary predator–prey models [7,16,32], but due to differences in subsystem stabilities and model dimension, it is unclear if the driving mechanisms are the same. Thus, theory is needed that explains how the speed of evolution interacts with subsystem stability to determine the stability of a whole system.

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 the unstable victim eco-evolutionary subsystems also had unstable victim evolutionary subsystems. Thus, instability of the eco-evolutionary subsystems must be due, in part, to the destabilizing effects of evolutionary feedbacks. Second, our approach may also be useful in purely ecological contexts. As examples, our approach could help identify how behavioural 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.

Data accessibility. Appendices uploaded as online supplementary materials. Maple, Matlab, and R computational code are publicly available at: http://doi.org/10.5281/zenodo.3530691.

Authors' contributions. All authors contributed to idea development and model analyses. M.H.C. wrote the first version of the manuscript and all authors contributed substantially to editing and revising.

Competing interests. We have no competing interests.

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