

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

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1        ABSTRACT: We develop a method to identify how ecological, evolutionary, and eco-  
2 evolutionary feedbacks influence system stability. We apply our method to nine empirically-  
3 parameterized eco-evolutionary models of exploiter-victim systems from the literature and  
4 identify which particular feedbacks cause some systems to converge to a steady state or  
5 to exhibit sustained oscillations. We find that ecological feedbacks involving the interac-  
6 tions between all species and evolutionary and eco-evolutionary feedbacks involving only  
7 the interactions between exploiter species (predators or pathogens) are typically stabilizing.  
8 In contrast, evolutionary and eco-evolutionary feedbacks involving the interactions between  
9 victim species (prey or hosts) are destabilizing more often than not. We also find that  
10 while eco-evolutionary feedbacks rarely altered system stability from what would be pre-  
11 dicted from just ecological and evolutionary feedbacks, eco-evolutionary feedbacks have the  
12 potential to alter system stability at faster or slower speeds of evolution. As the number  
13 of empirical studies demonstrating eco-evolutionary feedbacks increases, we can continue to  
14 apply these methods to determine whether the patterns we observe are common in other  
15 empirical communities.

## 16 Introduction

17 A fundamental problem in community ecology is understanding what factors influence system  
18 stability, e.g., whether a community converges to a steady state or exhibits cycles. Empir-  
19 ical and theoretical studies have shown that feedbacks between ecological and evolutionary  
20 processes, called eco-evolutionary feedbacks, can influence community stability and lead to  
21 different population-level dynamics (1; 2; 3; 4; 5; 6; 7). For example, experimental bacteria  
22 and virus-bacteria systems with demonstrated eco-evolutionary feedbacks converge to steady  
23 state (8; 9) whereas experimental rotifer-algae systems exhibit cycles (10; 11; 3; 12; 13).

24 Previous theoretical work has explored the (de)stabilizing effects ecological and evolu-  
25 tionary dynamics have on each other via eco-evolutionary feedbacks. In particular, ecological  
26 dynamics have the potential to stabilize unstable evolutionary dynamics or destabilize stable  
27 evolutionary dynamics (14; 2; 15). Similarly, evolutionary dynamics can stabilize or destabi-  
28 lize ecological dynamics (4; 5; 15). In general, stability of a whole system is influenced by the  
29 effects species' densities have on the dynamics of population densities (ecological feedbacks),  
30 the effects species' traits have on the dynamics of evolving traits (evolutionary feedbacks),  
31 and the effects population densities and evolving traits have on each other's dynamics (eco-  
32 evolutionary feedbacks). Previous theoretical work (7; 15; 16; 17) has explored when these  
33 feedbacks have stabilizing versus destabilizing effects, and shown that the strengths of those  
34 effects increase or decrease with changes in the relative rates of ecological and evolutionary  
35 change. Specifically, stability of the whole system in the slow evolution limit is determined  
36 by ecological and eco-evolutionary feedbacks whereas stability of the whole system in the  
37 fast evolution limit is determined by evolutionary and eco-evolutionary feedbacks.

38 While these theoretical results identify many possible outcomes, it is not well understood  
39 which particular feedbacks are responsible for causing stable versus cyclic population dy-  
40 namics in empirical systems. First, while the observed rates of ecological and evolutionary  
41 change are similar in the above empirical studies, most of the theory assumes ecological rates  
42 of change are either much faster or much slower than rates of evolutionary change. Second,

43 because most systems are not identical in their composition of species and traits, it is unclear  
44 how to make comparisons across systems. Third, many empirical systems involve multiple  
45 interacting species and multiple evolving traits, but because much of the theory focuses on  
46 models with a small number of species and traits, it is difficult to apply the theory. Thus,  
47 we need new theoretical tools that can extend current theory and identify broadly the effects  
48 of ecological, evolutionary, and eco-evolutionary feedbacks while simultaneously pinpointing  
49 the importance of particular feedbacks.

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

## 66 **Methods**

### 67 **Selecting parameterized eco-evolutionary models from published** 68 **studies**

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

### 82 **Method overview**

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

## 88 **A general eco-evolutionary model**

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

$$\begin{aligned}\frac{dN_i}{dt} &= f_i(N_1, \dots, N_n, x_1, \dots, x_m), \quad 1 \leq i \leq n \\ \frac{dx_j}{dt} &= g_j(N_1, \dots, N_n, x_1, \dots, x_m), \quad 1 \leq j \leq m.\end{aligned}\tag{1}$$

91 Here,  $f_i$  defines the ecological dynamics of species  $i$ ; it accounts for all (possibly trait-  
92 dependent) intra and interspecific interactions involving species  $i$  (e.g., cooperation, compe-  
93 tition, predation, and mutualism). The functions  $g_j$  define the evolutionary dynamics for  
94 each trait, which in general are density and frequency dependent. Note that clonal mod-  
95 els with two clonal types  $(C_1, C_2)$  can be converted into continuous trait models by deriving  
96 equations for the total density ( $N_1 = C_1 + C_2$ ) and the frequency of clone 1 ( $x_1 = C_1/N_1$ ); see  
97 appendix S2 for additional details. Model (1) has been used previously to study equilibrium  
98 stability and species coexistence (15; 22). It encompasses other bodies of eco-evolutionary  
99 theory based on adaptive dynamics (23; 24) and quantitative genetics (25).

## 100 **Complimentary subsystem pairs and subsystem stability**

101 We assume model (1) has a unique coexistence equilibrium where all species have positive  
102 densities; appendix S1 explains what changes when this assumption is not satisfied. We  
103 define stability of the whole system by the stability of the coexistence equilibrium, which  
104 is determined by the Jacobian ( $J$ ), i.e., a derivative matrix that determines whether small  
105 perturbations from equilibrium decay (implying stability) or grow (implying instability).  
106 Mathematically, for stable systems all eigenvalues of the Jacobian have negative real parts  
107 and for unstable systems the Jacobian has at least one eigenvalue with positive real part.  
108 Importantly, each empirically parameterized model we considered has a unique coexistence

109 equilibrium and if the coexistence equilibrium is unstable, then the system exhibits cycles  
 110 because the equilibrium underwent a Hopf bifurcation.

111 Our method focuses on the stabilities of complementary pairs of subsystems. A subsys-  
 112 tem describes the dynamics of a subset of variables when all other variables are fixed at  
 113 their equilibrium values. Two subsystems form a complementary pair if together the subsys-  
 114 tems include all variables in the system without overlap. For example, the ( $n$ -dimensional)  
 115 ecological subsystem describes the population dynamics of all species ( $dN_i/dt$  equations)  
 116 when all traits are fixed at their equilibrium values (solid box in figure 1B). Its complement  
 117 is the ( $m$ -dimensional) evolutionary subsystem (dashed box in figure 1B), which describes  
 118 the evolutionary dynamics of all traits ( $dx_j/dt$  equations) when all population densities are  
 119 fixed at their equilibrium values. Alternatively, an eco-evolutionary subsystem (solid box in  
 120 figure 1C) could be the population and trait dynamics associated with one species, say  $N_1$   
 121 and  $x_1$ . Its complementary subsystem (dashed box in figure 1C) is the population and trait  
 122 dynamics of the remaining species:  $N_2, \dots, N_n, x_2, \dots, x_m$ .

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

$$J = \begin{array}{cc} \text{Ecological Subsystem} & \text{Effects of Evo on Eco} \\ \left[ \begin{array}{c} \begin{array}{ccc} \frac{\partial}{\partial N_1} \frac{dN_1}{dt} & \frac{\partial}{\partial N_2} \frac{dN_1}{dt} & \frac{\partial}{\partial N_3} \frac{dN_1}{dt} \\ \frac{\partial}{\partial N_1} \frac{dN_2}{dt} & \frac{\partial}{\partial N_2} \frac{dN_2}{dt} & \frac{\partial}{\partial N_3} \frac{dN_2}{dt} \\ \frac{\partial}{\partial N_1} \frac{dN_3}{dt} & \frac{\partial}{\partial N_2} \frac{dN_3}{dt} & \frac{\partial}{\partial N_3} \frac{dN_3}{dt} \end{array} & \begin{array}{c} \frac{\partial}{\partial x_1} \frac{dN_1}{dt} \\ \frac{\partial}{\partial x_1} \frac{dN_2}{dt} \\ \frac{\partial}{\partial x_1} \frac{dN_3}{dt} \end{array} \\ \begin{array}{ccc} \frac{\partial}{\partial N_1} \frac{dx_1}{dt} & \frac{\partial}{\partial N_2} \frac{dx_1}{dt} & \frac{\partial}{\partial N_3} \frac{dx_1}{dt} \\ \frac{\partial}{\partial x_1} \frac{dx_1}{dt} & & \end{array} & \begin{array}{c} \frac{\partial}{\partial x_1} \frac{dx_1}{dt} \end{array} \end{array} \right] \\ \text{Effects of Eco on Evo} & \text{Evolutionary Subsystem} \end{array} \quad (2)$$

128 The top left box of the Jacobian determines the stability of the ecological subsystem (solid  
129 box in figure 1B), the bottom right box of the Jacobian determines the stability of the  
130 evolutionary subsystem (dashed box in figure 1B), and the off-diagonal boxes of the Jacobian  
131 determine the effects of ecology on evolution (bottom left) and the effects of evolution on  
132 ecology (top right). Mathematically, a subsystem is unstable if its submatrix has at least one  
133 eigenvalue with positive real part; a subsystem is stable if its submatrix has all eigenvalues  
134 with negative real parts; a subsystem is neutrally stable if its submatrix has all eigenvalues  
135 with non-positive real parts, at least one eigenvalue with strictly negative real part, and at  
136 least one eigenvalue with zero real part; and a subsystem is neutral if its submatrix has all  
137 eigenvalues with zero real parts; see figure S1 for illustrations of each type of stability.

## 138 **Stabilities of systems and their complimentary subsystem pairs**

139 When there are no feedbacks between a pair of complementary subsystems, the stability  
140 of the whole system is determined by the stabilities of the complementary subsystems: the  
141 whole system is stable if both subsystems are stable and the whole system is unstable (imply-  
142 ing cycles in our models) if either subsystem is unstable. When there are feedbacks between  
143 a pair of complementary subsystems, each subsystem has a stabilizing or destabilizing effect  
144 on the stability of whole system, but the feedbacks between the subsystems can alter the  
145 stability predicted by the complementary pair. For example, if the ecological subsystem is  
146 stable and the evolutionary subsystem is unstable in matrix (2), then the whole system is  
147 predicted to be unstable in the absence of eco-evolutionary feedbacks (zero entries in the top  
148 right or bottom left boxes). However, when eco-evolutionary feedbacks are present (non-zero  
149 entries in the top right and bottom left boxes) and stabilizing, the whole system can become  
150 stable. In this case, the feedbacks between the subsystems stabilize the whole system.

151 We consider four pairs of complementary systems, chosen for their biological relevance.  
152 First, the complementary ecological and evolutionary subsystems (figure 1B) identify the ef-  
153 fects of ecological, evolutionary, and eco-evolutionary feedbacks involving all species. Second,



154 the evolutionary subsystem for a single species (i.e., the subsystem composed of all evolving  
155 traits of one species) and its complement (also figure 1B) identify the effects of evolution-  
156 ary feedbacks of a single species. Third, the eco-evolutionary subsystem for a single species  
157 (i.e., the subsystem composed of the density and all evolving traits for that species) and its  
158 complement (figure 1C) identify the effects of feedbacks within a single species. Fourth, the  
159 subsystem defined by all species and traits in a particular trophic level and its complement  
160 (figure 1D) identify the effects of feedbacks within a particular trophic level.

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

168 Second, we compare the stabilities of the complementary subsystem pairs with the stabil-  
169 ity of the whole system in order to determine whether the feedbacks between subsystems do  
170 or do not alter system stability. There are four possibilities; the first and second correspond  
171 to cases where the feedbacks between complementary subsystems alter stability of the whole  
172 system from what would be predicted from just the stabilities of the complementary subsys-  
173 tems. First, if both subsystems are stable but the whole system is cyclic, then the feedbacks  
174 between the subsystems are destabilizing as they are sufficiently strong to counteract the  
175 stabilizing effects of the subsystems. Second, if one or both subsystems are unstable but the  
176 whole system is stable, then the feedbacks between the subsystems are stabilizing as they are  
177 sufficiently strong to counteract the destabilizing effects of the unstable subsystems. Third,  
178 if both subsystems are stable and the whole system is stable, then the feedbacks between  
179 the subsystems do not alter the stability of the system. Fourth, if one or both subsystems  
180 are unstable and the whole system is cyclic, then the feedbacks between the subsystems do

181 not alter the stability of the system.

## 182 **Effects of varied evolutionary speed**

183 To explore how the interactions between subsystem stability and the speed of evolution  
184 influence the stability of whole system, we varied the speed of evolution in the nine parame-  
185 terized models. This was done by introducing multiplicative parameters into the right hand  
186 sides of the trait equations in model (1); see appendix S3 for details. We then assessed how  
187 speeding up and slowing down the rates of evolution influenced system stability and whether  
188 stable versus cyclic dynamics in the whole system could be accurately predicted from just  
189 the stabilities of the ecological and evolutionary subsystems.

## 190 **Results**

### 191 **Effects of ecological, evolutionary and eco-evolutionary feedbacks** 192 **on the stabilities of empirical systems**

193 Across the nine parameterized models from the literature, subsystem stability differed de-  
194 pending on subsystem type (ecological, evolutionary, or eco-evolutionary) and species trophic  
195 level (exploiter vs. victim); see Table 1. Specifically, ecological subsystems were stable (or  
196 neutrally stable) in eight of the nine systems whereas evolutionary subsystems were stable  
197 in only four systems. Exploiter ecological, evolutionary, and eco-evolutionary subsystems  
198 were stable or neutral in seven systems. In contrast, victim ecological, evolutionary, and  
199 eco-evolutionary subsystems were stable in four systems.

200 With this information, we explored if feedbacks between subsystems altered the stability  
201 of the whole system from what would be predicted from just the stabilities of complementary  
202 subsystem pairs. What role do the feedbacks between subsystems play in influencing the  
203 stability of the four empirical systems that exhibit cycles (“cyclic” in column 4 of Table 1)?

204 First, the evolutionary subsystem was unstable in all four systems and the complementary  
205 ecological subsystem was stable in three systems. This means that the feedbacks between the  
206 ecological and evolutionary subsystems were insufficiently strong to stabilize the system. Sec-  
207 ond, the evolutionary and eco-evolutionary subsystems for the victim species were unstable  
208 in all four systems and their complementary subsystems were stable in three systems. This  
209 means that the feedbacks between the victim subsystems and their complementary subsys-  
210 tems were insufficiently strong to stabilize the system. Third, the evolutionary, evolutionary,  
211 eco-evolutionary subsystems for the exploiter species were stable or neutral in three of the  
212 studies and their complementary subsystems were stable in all four systems. This means  
213 that the feedbacks between the exploiter subsystems and their complementary subsystems  
214 were destabilizing and sufficiently strong to alter the stability of the whole system.

215 What role do the feedbacks between subsystems play in influencing the stability of the five  
216 empirical systems that converge to equilibrium (“stable” in column 4 of Table 1)? First, in  
217 two systems, all subsystems we considered were stable (21; 9). This means that all feedbacks  
218 between the subsystems were either stabilizing or insufficiently strong to destabilize the  
219 whole system. Second, in three systems, there was at least one complementary subsystem  
220 pair made up of one stable and one unstable subsystem. For each of those systems, the  
221 feedbacks between the complementary subsystems were stabilizing and sufficiently strong to  
222 stabilize the whole system. For example, while the prey evolutionary and eco-evolutionary  
223 subsystems were unstable in Kasada et al. (26), the whole system was stable because the  
224 feedbacks between those subsystems and their complements were strongly stabilizing.

## 225 **Effects of evolutionary speed on stability**

226 We explored how varying the speed of evolution affected system stability in the nine param-  
227 eterized models. If varying the speed of evolution causes a change in stability, then it either  
228 causes a system undergoing cycles to converge to equilibrium or it causes a stable system to  
229 exhibit cycles; see appendix S3 for mathematical details. Varying the speed of evolution in

230 the nine parameterized models produced one of four patterns (two shown in figure 2).

231 First, for the four systems with stable ecological subsystems and unstable evolutionary  
232 subsystems (S-U in “Eco & Evo” column of Table 1), stability of the whole system switched  
233 from stable to unstable as the speed of evolution increased (figure 2A-C). In these systems,  
234 cyclic dynamics in the fast evolution limit are expected due to the instability of the evolu-  
235 tionary subsystem. Stability in the slow evolution limit is caused by stabilizing feedbacks  
236 between the ecological and evolutionary subsystems that are sufficiently strong to counteract  
237 the instability of the evolutionary subsystem. Hence, feedbacks between the ecological and  
238 evolutionary subsystems do not alter the stabilities of these systems in the fast evolution  
239 limit, but they do stabilize the systems in the slow evolution limit.

240 Second, for the Haafke et al. (13) study where the ecological and evolutionary subsys-  
241 tems were both unstable, the whole system exhibited cycles for all evolutionary speeds. The  
242 presence of cycles for all evolutionary speeds implies that the feedbacks between the ecolog-  
243 ical and evolutionary subsystems did not alter the stability of the system for any speed of  
244 evolution.

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

250 Fourth, the Duffy et al. (27) system, where the ecological and evolutionary subsystems  
251 were both stable, the whole system was stable for very fast and very slow evolutionary  
252 speeds and unstable for intermediate evolutionary speeds (figure 2D-F). Instability of the  
253 whole system for intermediate evolutionary rates means that the feedbacks between the  
254 ecological and evolutionary subsystems were sufficiently strong to destabilize the system only  
255 for intermediate speeds of evolution. A similar pattern has been observed in eco-evolutionary  
256 predator-prey models (7; 30; 16), but it is unclear if the same mechanisms are driving the

257 pattern in the Duffy et al. (27) model because we lack general theory on when and why  
258 destabilization occurs at intermediate rates of evolution.

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

## 261 Discussion

262 Our results identified that ecological, evolutionary, and eco-evolutionary feedbacks have sys-  
263 tematically different effects on the stabilities of empirical systems and that those effects can  
264 depend on the species trophic level. Across the nine empirically parameterized models, eco-  
265 logical feedbacks tended to be stabilizing. In contrast, exploiter evolutionary feedbacks were  
266 stabilizing or neutral and victim evolutionary feedbacks were evenly split between stabilizing  
267 and destabilizing. Exploiter and victim ecological and eco-evolutionary feedbacks also con-  
268 sistently differed, with exploiter eco-evolutionary feedbacks being stabilizing or neutral and  
269 victim eco-evolutionary feedbacks being destabilizing more often than stabilizing. While our  
270 results are based on all empirically-parameterized models known to the authors, these models  
271 only represent a small number of systems, all of which involve exploiter-victim interactions.  
272 An important area of future work is applying and testing this theory in empirical systems  
273 with interactions other than exploiter-victim to understand whether ecological, evolutionary,  
274 and eco-evolutionary feedbacks have similar or different effects on stability in those systems.

275 Our results help elucidate why some eco-evolutionary systems converge to steady state  
276 whereas others exhibit sustained cycles. (Recall that for our nine parameterized models,  
277 instability of the coexistence equilibrium implies cyclic dynamics.) The evolutionary sub-  
278 systems were unstable in the four systems exhibiting cycles and stable in four of the five  
279 stable systems. This suggests that evolutionary feedbacks were important drivers of stabil-  
280 ity of our nine systems. In addition, in our models, instability and stability of evolutionary  
281 subsystems correspond to disruptive and stabilizing selection, respectively (2). Stabilizing

282 and disruptive selection are observed with roughly equal frequencies across a broad set of  
283 empirical systems (28), suggesting that the destabilizing effects of evolutionary feedbacks  
284 are widespread across empirical systems.

285 Our results also help identify when eco-evolutionary feedbacks do and do not alter stabil-  
286 ity. First, in all but one system, the stability of the whole system could be predicted from just  
287 the stabilities of the ecological and evolutionary subsystems, implying eco-evolutionary feed-  
288 backs between all species did not alter the stability of the whole system. The one exception  
289 is the Kasada et al. (26) study, where we predict the eco-evolutionary feedbacks stabilized  
290 the whole system. Second, our results show that eco-evolutionary feedbacks involving just  
291 a subset of the species in the community could have different effects on stability. In par-  
292 ticular, the eco-evolutionary feedbacks between the densities and traits of victim species  
293 could be stabilizing or destabilizing. This is consistent with prior theory predicting prey  
294 eco-evolutionary feedbacks can be stabilizing or destabilizing (2; 4; 7). In contrast, we found  
295 that the eco-evolutionary feedbacks between the densities and traits of exploiter species  
296 were stabilizing. Current theory predicts predator eco-evolutionary feedbacks can also be  
297 destabilizing (29; 30), but this was not observed in the four systems with exploiter evolution.

298 Our predictions about subsystem stability can be tested in empirical systems through  
299 controlled experiments in which some variables are held (nearly) fixed at their equilibrium  
300 values. One way to effectively fix evolutionary variables is to seed populations with lower  
301 standing genetic variation, e.g., as in (31; 3; 32; 33). If the magnitude of genetic variation  
302 is varied while the mean trait value is kept (effectively) constant, then the low genetic  
303 variation treatment will yield information about the stability of subsystems without that  
304 trait. Similarly, holding a species' density nearly fixed will yield information about the  
305 stabilities of subsystems without that species. However, in most cases, subsystem stability  
306 cannot be determined by experiments where a variable is removed or changed substantially  
307 from its equilibrium value (e.g., removing a predator). This is because our subsystem-  
308 based approach assumes all fixed variables are held at their equilibrium values. It may

309 be difficult or infeasible to hold densities or traits (nearly) constant in a given empirical  
310 system. Nonetheless, applying our theory to tailored, parameterized models allows one to  
311 make predictions about how specific feedbacks influence community stability and dynamics.

312 Our results highlight the need for additional theory to explain how the relative rates of  
313 evolution and ecology influence system stability. First, following Cortez (16), our approach  
314 can be extended to consider the effects of all subsystems. However, in systems with many  
315 species, the number of subsystems becomes very large, e.g., the Wei et al. (34) model with  
316 10 variables has 1023 subsystems. Thus, new theory is needed to help understand what  
317 general rules govern how and when different subsystems influence system stability. Second,  
318 while current theory (7; 30; 16; 15) can explain model stability in the fast and slow evolution  
319 limits, we have a limited ability to make predictions about system stability when rates of  
320 ecology and evolution are similar. For example, it is unclear why the Duffy et al. (27) model  
321 exhibits cycles only at intermediate evolutionary speeds (figure 2D-F). This pattern has  
322 been observed in eco-evolutionary predator-prey models (7; 30; 16), but due to differences  
323 in subsystem stabilities and model dimension, it is unclear if the driving mechanisms are  
324 the same. Thus, theory is needed that explains how the speed of evolution interacts with  
325 subsystem stability to determine the stability of a whole system.

326 Our subsystem-based approach can be extended and potentially fruitful in other areas.  
327 First, applying our approach to a particular subsystem can help determine what feedbacks  
328 within that subsystem are responsible for its stability. For example, nearly all systems  
329 with unstable victim eco-evolutionary subsystems also had unstable victim evolutionary  
330 subsystems. Thus, instability of the eco-evolutionary subsystems must be due, in part, to  
331 the destabilizing effects of evolutionary feedbacks. Second, our approach may also be useful  
332 in purely ecological contexts. As examples, our approach could help identify how behavioral  
333 dynamics and species abundance dynamics affect community stability, how feedbacks within  
334 and between trophic levels affect the stability of food webs, how within-soil and above-soil  
335 communities contribute to the stability of plant-soil communities, and how environmental

336 dynamics and species abundance dynamics affect system stability.

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340

## 341 **Data Accessibility**

342 Appendices uploaded as online supplementary materials.

343 Computational files: zenodo DOI 10.5281/zenodo.3530691

344

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428 **Tables and Figures**

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

Study	Evolving	System	Stabilities of complementary subsystem pairs*				
	Species	Behavior	Eco & Evo	Victim evo	Victim eco or eco-evo <sup>†</sup>	Exploiter Evo	Exploiter eco or eco-evo <sup>†</sup>
<u>Predator-prey</u>							
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. (26)	Prey	Stable	S - U	U - S	U - S		N - U
Wei et al. (34) Fig. 5a	Both	Stable	S - S	S - S	S - S	N - S	N - S
430 Fig. 5b	Both	Stable	S - S	S - U	U - S	N - S	N - U
Yoshida et al. (11; 10)	Prey	Cyclic	S - U	U - S	U - S		S - U
<u>Intraguild predation</u>							
Hiltunen et al. (35) <sup>‡</sup> Fig. 2.1b	Basal prey	Cyclic	S - U	U - S	U - S		S - U
Fig. 2.1c	Basal prey	Cyclic	S - U	U - S	U - U		U - U
Fig. 2.1d	Basal prey	Cyclic	S - U	U - S	U - S		S - U
<u>Host-parasite</u>							
Bolker et al. (21)	Parasite	Stable	S - S		S - S	S - S	S - S
Duffy et al. (27)	Host	Stable	S - S	S - S	S - S		U - S

431

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

433 affect the stability of the whole system (S= stabilizing, U = destabilizing, N = neutral effect, Eco = ecological, Evo = evolu-

434 tionary, Eco-evo = eco-evolutionary).

435 † In systems without victim (exploiter) evolution, the victim (exploiter) eco-evolutionary and ecological systems are the same.  
436 ‡ Victim subsystems only involve the basal prey variables and exploiter subsystems involve the intraguild prey and intraguild  
437 predator variables.

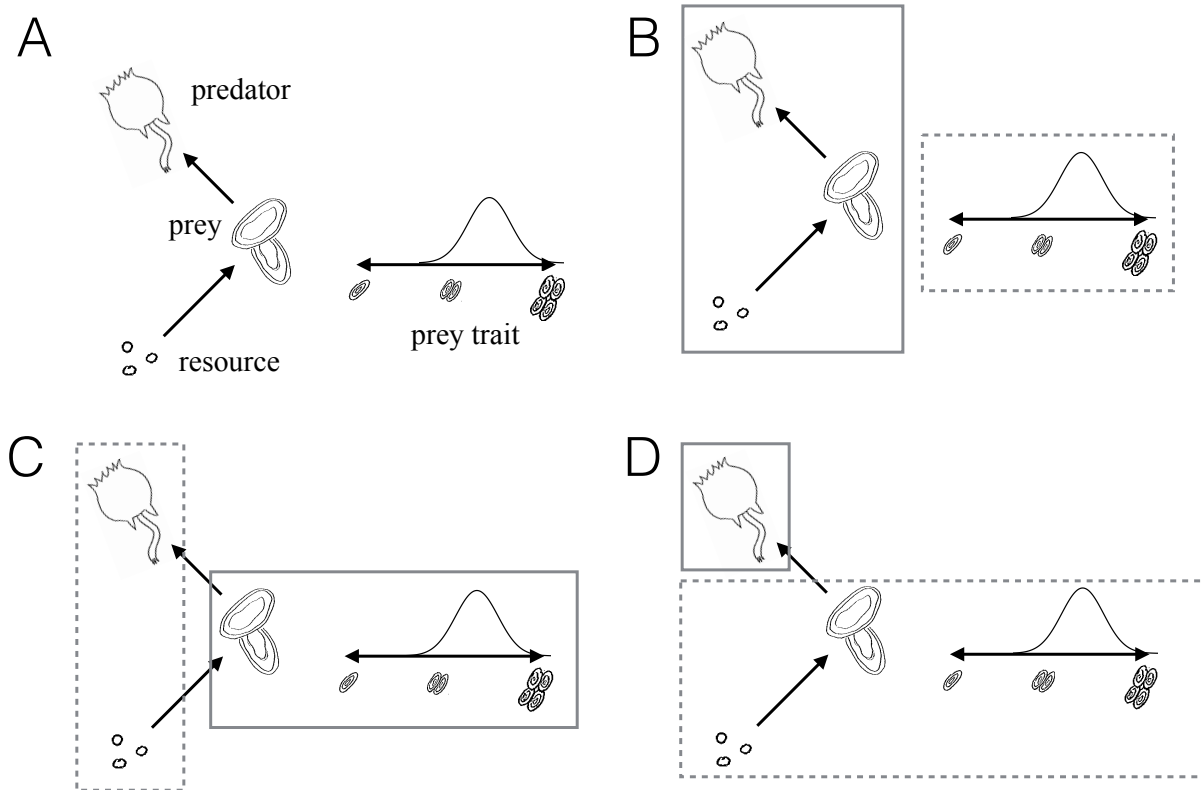


Figure 1: Examples of complementary subsystem pairs in the resource-prey-predator system with an evolving prey trait from Becks et al. (3). (A) The system dynamics involve changes in resource (nitrogen), prey (algae), and predator (rotifers) densities and the mean clump size of the prey. (B) Ecological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

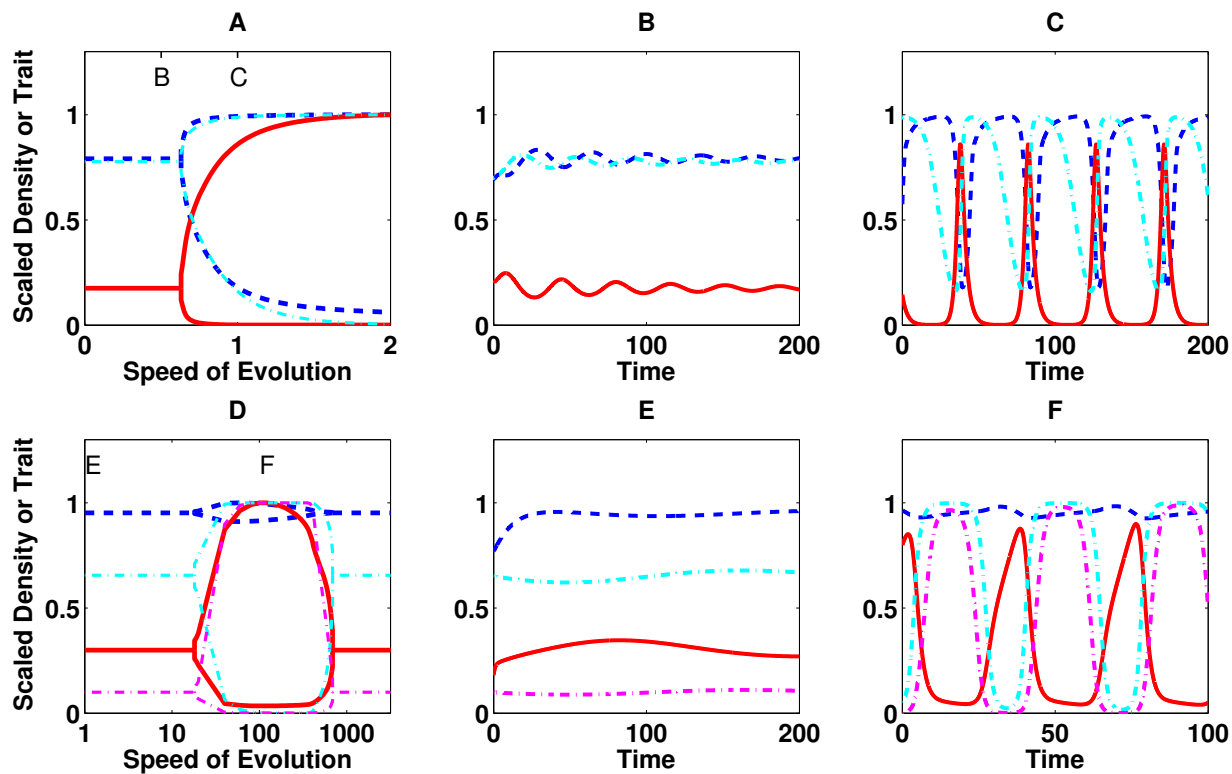


Figure 2: Predicted stability and dynamics of eco-evolutionary models with increased or decreased rates of evolution. (A-C) Dynamics of the Becks et al. (3) model with prey density (dashed blue), predator density (solid red), and proportion of defended prey (dash-dot cyan); nutrient dynamics are not shown. (D-F) Dynamics of the Duffy et al. (27) 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.

438 **Supplementary Information for ‘Destabilizing evolution-**  
439 **ary and eco-evolutionary feedbacks drive eco-evo cycles**  
440 **in empirical systems’**

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## 458 S1 Notation, subsystems, and stability

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

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

463 The equilibrium is stable if all eigenvalues of  $J$  have negative real parts, neutrally stable  
 464 if all eigenvalues have non-positive real parts and at least one eigenvalue has negative real  
 465 part, neutral if all eigenvalues have zero real parts, and unstable if at least one eigenvalue  
 466 has positive real part. See figure S1 for an illustration of these definitions.

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

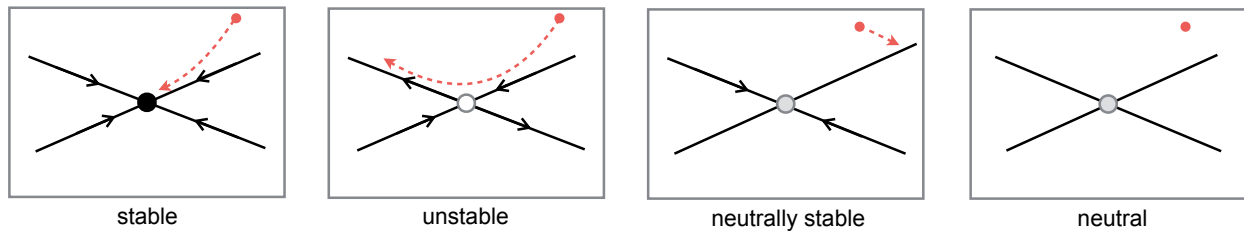


Figure S1: Two-dimensional examples of stable, unstable, neutrally stable, and neutral equilibria. Black lines are the eigenvectors computed from the Jacobian evaluated at the equilibrium. Black arrows denote the direction of the flow along the eigenvectors; an eigenvector with no arrow means no flow in that direction. Red dashed curves are example trajectories starting at the red dots.

470 eigenvalues of  $M_S$  following the same rules used for the coexistence equilibrium. Ecological  
471 subsystems contain only ecological variables ( $N_i$ ). Evolutionary subsystems contain only  
472 evolutionary variables ( $x_j$ ). Eco-evolutionary variables contain ecological and evolutionary  
473 variables. Two subsystems  $S_1$  and  $S_2$  form a complementary pair if their intersection is the  
474 empty set and their union contains all variables in the system.

475 In general, the stabilities of the subsystems influence the stability of the coexistence  
476 equilibrium. We begin by illustrating this in a two-dimensional system and then show how  
477 the idea extends to higher-dimensions. Consider a model with one ecological variable ( $N$ )  
478 and one evolutionary variable ( $x$ ). Such a model has a 2x2 Jacobian ( $J$ ) where the stability  
479 of the ecological subsystem is determined by the  $J_{11}$  entry, the stability of the evolutionary  
480 subsystem is determined by the  $J_{22}$  entry, and the interactions between the subsystems are  
481 defined by the product  $J_{12}J_{21}$ . When  $J_{11} < 0$ , the ecological subsystem has a stabilizing  
482 effect on the stability of the equilibrium and when  $J_{11} > 0$ , the ecological subsystem has a  
483 destabilizing effect on the stability of the equilibrium. Similarly, when  $J_{22} < 0$  or  $J_{22} > 0$ , the  
484 evolutionary subsystem has a stabilizing or destabilizing effect, respectively, on the stability  
485 of the equilibrium. In the absence of bidirectional feedbacks between the ecological and  
486 evolutionary subsystems (i.e.,  $J_{12}J_{21} = 0$ ), the stability of the equilibrium is determined by  
487 the stability of the ecological and evolutionary subsystems. However, when bidirectional  
488 feedbacks are present, the interactions between the two subsystems have stabilizing effects

489 when  $J_{12}J_{21} > 0$  and destabilizing effects when  $J_{12}J_{21} < 0$ .

490 A similar idea holds in higher dimensional models, where the entries  $J_{11}$  and  $J_{22}$  are re-  
491 placed by submatrices of the Jacobian corresponding to a pair of complementary subsystems.  
492 The entries  $J_{12}$  and  $J_{21}$  are replaced by submatrices that represent the effects variables in one  
493 subsystem have on the dynamics of the variables in the other subsystem. Thus, stability of  
494 an equilibrium is affected by the stability of each subsystem as well as the feedbacks between  
495 the subsystems.

496 To show how stable, neutrally stable, neutral, and unstable subsystems influence equi-  
497 librium stability in higher dimensional models, we use the characteristic polynomial of  
498 the Jacobian. As an example consider a four dimensional system with variables  $N_1, N_2, N_3$   
499 and  $x_1$ . The characteristic polynomial of the Jacobian ( $J$ ) for such a system is

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

where

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

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

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

where

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

504 A necessary condition for stability of the ecological subsystem is  $b_i > 0$  for all  $i$ . Notice that  
505 each term in the  $b_1$  equation also shows up in the equation for  $a_1$ . More generally,  $b_i$  is a  
506 partial sum of the terms that define  $a_i$ .

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

519 The above argument holds for a Jacobian of any size and a submatrix of any size. It  
520 explains our interpretation of how subsystems with different stabilities affect equilibrium  
521 stability. The above only focuses on the necessary condition for stability, i.e., all coefficients  
522 of the characteristic polynomial are positive. Necessary and sufficient conditions for stability  
523 are defined by the Routh-Hurwitz criteria. We do not use all of the conditions from the  
524 Routh-Hurwitz criteria because the other conditions are more complex and less tractable for  
525 large matrices.

## 526 **S2 Complementary subsystem pairs method**

527 Here we detail how one can apply our complementary subsystem method to their own mode.

528 Note that Step 1 is skipped for models with continuous traits.

529

### 530 **Step 1: Convert discrete trait model into continuous trait model**

531 For clonal models without stage structure where  $C_i$  is the density of clone  $i$ , the ecological  
532 variable of the continuous trait model is total density,  $N = \sum_i C_i$ , and the evolutionary  
533 variables are the frequencies of clone  $i$ ,  $x_i = C_i/N$ , for  $i < k$ . For clonal models with stage  
534 structure where  $C_i^j$  is the density of clone  $i$  in stage  $j$ , the ecological variables are the total  
535 densities in each stage,  $N_j = \sum_j C_i^j$ , and the evolutionary variables are the proportions of  
536 clone  $i$  in each stage,  $C_i^j/N_j$  for  $i > 1$ . The differential equations for the continuous trait  
537 model are derived using the chain rule, e.g.,  $dN/dt = \sum_i \frac{dC_i}{dt}$  and  $dx_i/dt = (N \frac{dC_i}{dt} - C_i \frac{dN}{dt})/N^2$   
538 define the dynamics for a continuous trait model derived from a clonal model without stage  
539 structure.

### 540 **Step 2: Find coexistence equilibria and determine their stability**

541 For each coexistence equilibrium,  $\rho$ , stability is determined by computing the eigenvalues of  
542 the Jacobian evaluated at  $\rho$ .

### 543 **Step 3: Pick a complementary subsystem pair and determine stabilities of the** 544 **subsystems**

545 Partition the state variables into two complementary. Let  $S_1$  be the subsystem containing  
546 variables from the first subset and  $S_2$  be the subsystem containing variables from the second  
547 subset. Find the two submatrices of the Jacobian corresponding to the two subsystems. In  
548 particular, the submatrix corresponding to subsystem  $S_1$  is made up of all entries  $\partial \dot{s}_i / \partial s_j$   
549 ( $s_i, s_j \in S_1$ ) and the submatrix corresponding to subsystem  $S_2$  is made up of all entries  
550  $\partial \dot{s}_i / \partial s_j$  ( $s_i, s_j \in S_2$ ). For each coexistence equilibrium, evaluate the two submatrices at the  
551 equilibrium and determine the stability of each subsystem by finding the eigenvalues of each  
552 submatrix.

553 **Step 4: Compare stabilities of whole system and subsystem pairs**

554 For each coexistence equilibrium, compare its stability with the stability of the comple-  
555 mentary subsystems. If (i) both subsystems are stable and the coexistence equilibrium is  
556 unstable, (ii) both subsystems are unstable and the coexistence equilibrium is stable, or (iii)  
557 one subsystem is unstable, one subsystem is stable, and the coexistence equilibrium is stable,  
558 then the stability of the coexistence equilibrium differs from what is predicted from just the  
559 stabilities of the complementary subsystems. In such cases, the interactions between the  
560 subsystems alter the stability of the coexistence equilibrium based on what is predicted from  
561 just the stabilities of the complementary subsystems. In all other cases, the interactions  
562 between subsystems do not alter the stability of the coexistence equilibrium based on what  
563 is predicted from just the stabilities of the complementary subsystems.

564

565 We note two things about applying our method. First, applying our method to an un-  
566 stable equilibrium (i.e., an equilibrium whose Jacobian has at least one eigenvalue with  
567 positive real part) will identify which feedbacks are destabilizing that particular equilibrium.  
568 However, it may not explain why cyclic dynamics occur in that system, e.g., when there  
569 are unstable equilibria with homoclinic or heteroclinic orbits or cycles that arose via bifurca-  
570 tions not involving equilibria. Information about equilibrium instability is informative about  
571 cyclic dynamics only if the equilibrium has undergone a Hopf bifurcation that gave rise to  
572 an attracting periodic orbit (as was the case for the empirically parameterized models we  
573 considered).

574 Second, applying our method to a coexistence equilibrium always identifies how feedbacks  
575 affect stability at that specific equilibrium. However, if multiple equilibria are present, the  
576 feedbacks may have different effects at different equilibria. This is expected because the trait  
577 values and densities differ between the equilibria. However, it means that judgment must be  
578 used to determine which equilibria will yield biologically informative information. Applying  
579 our method to a stable coexistence equilibrium is always biologically informative because it

580 identifies which feedbacks are responsible for stabilizing the system near that equilibrium.  
581 For unstable equilibria, our results are biologically informative if (i) the unstable equilibrium  
582 and an attracting periodic orbit are both present for the given parameter values and (ii) the  
583 unstable manifold of the equilibrium point intersects the stable manifold of the periodic  
584 orbit. In this case, our results help explain which feedbacks are responsible for destabilizing  
585 the unstable equilibrium and causing the system to exhibit periodic cycles. In other cases,  
586 e.g., when there are no periodic orbits or the equilibria have homoclinic or heteroclinic  
587 connections, applying our method to unstable equilibria may not explain system behavior.

### 588 **S3 Varying evolutionary speeds**

589 To vary the speed of evolution in the models, we multiplied the right hand sides of the trait  
590 equations by the parameter  $\epsilon_i$ , where the rate of evolution is unchanged for  $\epsilon_i = 1$  and is  
591 slowed down (sped up) for  $0 < \epsilon_i < 1$  ( $\epsilon_i > 1$ ). For example, the trait dynamics  $dx_1/dt = g(\cdot)$   
592 are changed to  $dx_1/dt = \epsilon_1 g(\cdot)$ . For systems where a single species had multiple traits,  
593 each trait equation was multiplied by the same parameter (e.g.,  $\epsilon_1$  for all trait equations).  
594 For systems with multiple evolving species, the trait equations for different species were  
595 multiplied by different parameters (e.g.,  $\epsilon_1$  for the prey trait and  $\epsilon_2$  for the predator trait).  
596 Our analysis only focused on the effects of varying each  $\epsilon_i$  parameter independently; we did  
597 not explore how simultaneously varying multiple  $\epsilon_i$  parameters would affect system stability.

598 Multiplying a trait equation by  $\epsilon_i$  results in each entry of the Jacobian corresponding  
599 to that trait equation being multiplied by  $\epsilon_i$ . Thus, varying  $\epsilon_i$  changes the magnitudes of  
600 those Jacobian entries, which in turn affects the eigenvalues of the Jacobian. For all of the  
601 models we considered, changing the rate of evolution (i.e., varying  $\epsilon_i$ ) does not change the  
602 location of an equilibrium point. Thus, varying  $\epsilon_i$  does not affect the entries of the Jacobian  
603 corresponding to the ecological equations or other trait equations.

604 For all models we considered, equilibria can only undergo Hopf bifurcations as the  $\epsilon_i$

605 parameters are varied (15), and they cannot undergo bifurcations where one or more eigen-  
606 values are identically zero. The mathematical justification is the following. The determinant  
607 of the Jacobian factors as  $|J| = \epsilon_i |J_{\epsilon_i=1}|$  where  $|J_{\epsilon_i=1}|$  is the determinant of the Jacobian  
608 when  $\epsilon_i = 1$ . Recall that the determinant of a matrix is equal to the product of its eigenval-  
609 ues. If the equilibrium were to undergo a bifurcation with a zero eigenvalue, then  $|J_{\epsilon_i}| = 0$   
610 for some  $\epsilon_i$  value, which would imply  $|J_{\epsilon_i=1}| = 0$  and further that  $|J_{\epsilon_i}| = 0$  for all  $\epsilon_i > 0$ .  
611 Thus, the sign of  $|J|$  is constant for  $\epsilon_i > 0$ . This means that the eigenvalues of  $|J|$  can only  
612 change signs via Hopf bifurcations. In total, increasing or decreasing the rate of evolution  
613 can cause no effect on stability or cause the periodic orbit to undergo a Hopf bifurcation,  
614 i.e., either cause a system undergoing oscillations to converge to an equilibrium or cause a  
615 stable system to exhibit cycles.

## 616 **S4 Analysis of parameterized models**

617 Here, we analyze the nine empirically parameterized models from the literature; subsystem  
618 stabilities are given in table S1. All calculations can be reproduced using the accompanying  
619 Maple worksheet and R files. However, the results for subsystem stability differ between  
620 the Maple worksheet and R files because of small numerical errors in R that result in R  
621 computing non-zero values for Jacobian entries that are analytically zero. If these numerical  
622 errors are accounted for (i.e., the entries are set equal to zero), then the results from R and  
623 Maple agree. In the following, Jacobian entries are listed as zero only if it is possible to show  
624 analytically that the entry is zero (see Maple worksheet for details). All other entries are  
625 rounded to three significant digits.



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

Study	Evolving Species	System Behavior	Stabilities of complementary subsystem pairs*				
			Eco & Evo	Prey evo	Prey eco or eco-evo <sup>†</sup>	Pred Evo	Pred eco or eco-evo <sup>†</sup>
<u>Predator-prey</u>							
Becks et al. (3)	Prey	Cyclic	S - U	U - S	U - NS		NS - U
Frickel et al. (9)	Both	Stable	S - S	S - S	NS - NS	S - S	NS - S
Haafke et al. (13)	Both	Cyclic	U - U	U - U	U - NS	NS - U	NS - U
Kasada et al. (26)	Prey	Stable	S - U	U - S	U - NS		N - U
Wei et al. (34) Fig. 5a	Both	Stable	S - S	S - NS	S - NS	N - S	N - S
627 Fig. 5b	Both	Stable	S - S	S - U	U - NS	N - S	N - U
Yoshida et al. (11; 10)	Prey	Cyclic	S - U	U - S	U - NS		NS - U
<u>Intraguild predation</u>							
Hiltunen et al. (35) <sup>‡</sup> Fig. 2.1b	Basal prey	Cyclic	S - U	U - S	U - S		S - U
Fig. 2.1c	Basal prey	Cyclic	S - U	U - S	U - U		U - U
Fig. 2.1d	Basal prey	Cyclic	S - U	U - S	U - S		S - U
<u>Host-parasite</u>							
Bolker et al. (21)	Parasite	Stable	S - S		S - NS	S - S	NS - S
Duffy et al. (27)	Host	Stable	S - S	S - S	S - S		U - S

628  
 629 \* The first letter is the stability of the subsystem listed in the column and the second is the stability of the complemen-  
 630 tary subsystem. S = all eigenvalues for the submatrix have negative real part; U = at least one eigenvalue has positive real  
 631 part; NS = at least one eigenvalue has negative real part and at least one eigenvalue is zero; N = all eigenvalues are zero. Eco  
 632 = ecological subsystem; Evo = evolutionary subsystem; Eco-evo = eco-evolutionary subsystem; Pred = exploiter (predator or  
 633 pathogen); Prey = victim (prey or host).

634 <sup>†</sup> For systems without prey (predator) evolution, the prey (predator) eco-evolutionary subsystem is just the prey (predator)  
 635 ecological subsystem.

636 <sup>‡</sup> Prey subsystems refer to subsystems with just the basal resource variables and predator subsystems refer to subsystems with  
 637 both the intraguild prey and the intraguild predator variables.

### 638 S4.1 Becks et al. (3) Model

The discrete trait model is

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

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

643 The four ecological variables for the continuous trait model are  $N$ ,  $C = C_1 + C_2$ ,  $B$ , and  $S$ ,  
 644 and the single evolutionary variable is  $x_1 = C_1/C$ . The equilibrium of the continuous trait  
 645 model is  $(N, C, B, S, x_1) = (5.91, 0.338, 2.49, 2.8, 0.777)$ . The Jacobian for the continuous  
 646 trait model is

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

647 where the order of the rows and columns is  $(N, C, B, S, x_1)$ . The eigenvalues are  
 648  $(-3.58, -0.462, -0.23, 0.0219 \pm 0.229i)$ , which implies the equilibrium is unstable. The insta-  
 649 bility of the equilibrium is due to a Hopf bifurcation that occurs at  $\delta \approx 0.55$ . The stabilities  
 650 of the complementary pairs are given in Table S2.

651 **Table S2:** Stabilities of subsystems for the Becks et al. (3) model

Subsystem	Variables	Eigenvalues	Stability
Ecological	$\{N, C, B, S\}$	$-3.57, -0.123 \pm 0.109, -0.455$	stable
Evolutionary	$\{x_1\}$	0.0436	unstable
Prey evo	$\{x_1\}$	0.0436	unstable
652 Complement	$\{N, C, B, S\}$	$-3.57, -0.123 \pm 0.109, -0.455$	stable
Prey eco-evo	$\{C, x_1\}$	$-2.24 \cdot 10^{-11}, 0.0716$	unstable
Complement	$\{N, B, S\}$	$0, -3.941, -0.355$	neutrally stable
Predator eco	$\{B, S\}$	$0, -0.355$	neutrally stable
Complement	$\{N, C, x_1\}$	$-3.58, -0.336, 0.042$	unstable

## 653 S4.2 Bolker et al. (21) Model

The model is

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

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

663 The equilibrium for the SARS parameterization is  $(S, I, \alpha) = (0.333, 0.00104, 640)$ ; the  
 664 equilibrium for the HIV parameterization is  $(S, I, \alpha) = (.699, 0.0409, 6.36)$ ; the equilibrium  
 665 for the WNV parameterization is  $(S, I, \alpha) = (.309, 0.001082, 639)$ ; and the equilibrium for  
 666 the Myx parameterization is  $(S, I, \alpha) = (1/3, 1/9, 5)$ . The Jacobians for the different param-  
 667 eterizations are

$$J_{SARS} = \begin{pmatrix} -3 & -641 & -0.09 \\ 2 & 0 & 0 \\ 3 & 0 & -2.44 \cdot 10^{-6} \end{pmatrix}, \quad J_{HIV} = \begin{pmatrix} -1.43 & -7.36 & -0.0409 \\ 0.43 & 0 & 0 \\ 1.43 & 0 & -0.0214 \end{pmatrix}\tag{S.9}$$

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

668 where the orders of the columns and rows are  $(S, I, \alpha)$ . The eigenvalues of  $J_{SARS}$  are  
669  $(-1.5 \pm 35.8i, -2.44 \cdot 10^{-6})$ ; the eigenvalues of  $J_{HIV}$  are  $(-0.715 \pm 1.65i, -0.021)$ ; the  
670 eigenvalues of  $J_{WNV}$  are  $(-1.62 \pm 37.8i, -2.45 \cdot 10^{-6})$ ; and the eigenvalues of  $J_{Myx}$  are  
671  $(-1.5 \pm 3.18i, -0.0324)$ . In all cases the equilibria are stable. The stabilities of the com-  
672plementary pairs are given in Table S3. Note that the ecological subsystem  $\{S, I\}$  and the  
673 complementary evolutionary subsystem is  $\{\alpha\}$  also define the parasite evolutionary subsys-  
674tem and its complement.

675 **Table S3:** Stabilities of subsystems for the Bolker et al. (21) model

	Subsystem	Variables	Eigenvalues	Stability
<b>WNV</b>	Ecological	$\{S, I\}$	$-1.5 \pm 35.8i$	stable
	Evolutionary	$\{\alpha\}$	$-2.44 \cdot 10^{-6}$	stable
	Parasite eco-evo	$\{I, \alpha\}$	$0, -2.44 \cdot 10^{-6}$	neutrally stable
	Complement	$\{S\}$	$-3$	stable
<b>HIV</b>	Ecological	$\{S, I\}$	$-0.715 \pm 1.65i$	stable
	Evolutionary	$\{\alpha\}$	$-0.021$	stable
	Parasite eco-evo	$\{I, \alpha\}$	$0, -0.021$	neutrally stable
	Complement	$\{S\}$	$-1.43$	stable
<b>SARS</b>	Ecological	$\{S, I\}$	$-1.62 \pm 37.8i$	stable
	Evolutionary	$\{\alpha\}$	$-2.45 \cdot 10^{-6}$	stable
	Parasite eco-evo	$\{I, \alpha\}$	$0, -2.45 \cdot 10^{-6}$	neutrally stable
	Complement	$\{S\}$	$-3.24$	stable
<b>Myx</b>	Ecological	$\{S, I\}$	$-1.5 \pm 3.18i$	stable
	Evolutionary	$\{\alpha\}$	$-0.0333$	stable
	Parasite eco-evo	$\{I, \alpha\}$	$0, -0.0333$	neutrally stable
	Complement	$\{S\}$	$-3$	stable

676

### 677 S4.3 Duffy et al. (27) Model

The model is

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

678 where  $S_i$  and  $I_i$  are the densities of susceptible and infected clonal hosts ( $i = 1, 2$ ), re-  
 679 spectively, and  $Z$  is the spore density. The parameter values for the model are  $b_1 =$   
 680  $5712.11\beta_1 + 0.241$ ,  $b_2 = 5712.11\beta_2 + 0.241$ ,  $d = 0.05$ ,  $e = 0.5$ ,  $f = 0.75$ ,  $K = 5$ ,  $m = 0.1$ ,  
 681  $n = 0.05$ ,  $v = 0.05$ ,  $\beta_1 = 0.5 \cdot 10^{-6}$ ,  $\beta_2 = 8.5 \cdot 10^{-6}$ ,  $\theta = 9$ ,  $\sigma = 15000$ .

682 The three ecological variables for the continuous trait model are  $S = S_1 + S_2$ ,  $I = I_1 + I_2$ ,  
 683 and  $Z$  and the evolutionary variables are the proportions of host clone one in each stage,  
 684  $x_1 = S_1/S$  and  $x_2 = I_2/I$ . The equilibrium of the continuous trait model is  $(S, I, Z, x_1, x_2) =$   
 685  $(1.86, 0.025, 4120, 0.656, 0.101)$ . The Jacobian for the continuous trait system is

$$\begin{pmatrix}
 -0.0995 & 0.0353 & -6.06 \cdot 10^{-6} & 0.00838 & -0.000533 \\
 0.0134 & -1 & 6.06 \cdot 10^{-6} & -0.0614 & 0 \\
 -0.0134 & 8250 & -0.05 & 0.0614 & 0 \\
 0.00294 & -0.0383 & 1.806 \cdot 10^6 & -0.00318 & 0.00171 \\
 0 & 0 & 0 & 0.401 & -1
 \end{pmatrix}
 \tag{S.12}$$

686 where the order of the rows and columns is  $(S, I, Z, x_1, x_2)$ . The eigenvalues are  
 687  $(-1.05, -1, -0.0915, -0.00318 \pm 0.027i)$ , which implies the equilibrium is stable. The sta-  
 688 bilities of the complementary pairs are given in Table S4.

689 **Table S4:** Stabilities of subsystems for the Duffy et al. (27) model

Subsystem	Variables	Eigenvalues	Stability
Ecological	$\{S, I, Z\}$	$-1.05, -0.091, -0.00671$	stable
Evolutionary	$\{x_1, x_2\}$	$-0.00249, -1$	stable
Host evo	$\{x_1, x_2\}$	$-0.00249, -1$	stable
690 Complement	$\{S, I, Z\}$	$-1.05, -0.091, -0.00671$	stable
Host eco-evo	$\{S, I, x_1, x_2\}$	$-0.0991, -1.49, -1.00, -1$	stable
Complement	$\{Z\}$	$-0.05$	stable
Parasite eco	$\{I, Z\}$	$-1.05, 1.19$	unstable
Complement	$\{S, x_1, x_2\}$	$-0.0998, -0.00225, -1$	stable



## 691 S4.4 Frickel et al. (9) Model

692 In matrix form the model is

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

693 where  $S$  is the resource concentration,  $\vec{B} = (B_1, B_2, B_3, B_4)$  is the density of algal clones,  
 694 and  $\vec{P} = (P_1, P_2, P_3)$  is the density of viral types. In the model,  $*$  denotes component-wise  
 695 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  
 696 triangular 4x3 matrix with ones on and above the main diagonal. The matrices  $M_B$  and  $M_P$   
 697 are

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

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

700 The three ecological variables for the continuous trait model are  $S$ , total algal density  
 701 ( $B = B_1 + B_2 + B_3 + B_4$ ), and total viral density ( $P = P_1 + P_2 + P_3$ ). The evolutionary  
 702 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 equilibrium  
 703 of the continuous trait model is  $(S, B, P, x_1, x_2, x_3, x_4, x_5)$   
 704  $= (2.01, 1210000, 0.00884, 0.726 \cdot 10^{-4}, 0.00224, 889000, 0.973 \cdot 10^{-5}, 0.005)$ . The Jacobian is

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

705 where the order of the columns and rows is  $(S, B, P, x_1, x_2, x_3, x_4, x_5)$ . The eigenvalues are  
 706  $(-0.463, -0.00437 \pm 0.0792i, -0.1, -0.0365, -0.0204, -0.0207, -0.0222)$ , which implies the  
 707 equilibrium is stable. The stabilities of the complementary pairs are given in Table S5.

708 **Table S5:** Stabilities of subsystems for the Frickel et al. (9) model

Subsystem	Variables	Eigenvalues	Stability
Ecological	$\{S, B, P\}$	$-0.463, -0.1, -0.000905$	stable
Evolutionary	$\{x_1, x_2, x_3, x_4, x_5\}$	$-5.11 \cdot 10^{-8}, -0.0439, -0.0222, -0.0203, -0.0208$	stable
Prey evo	$\{x_1, x_2, x_3\}$	$-5.0610 \cdot 10^{-8}, -0.0222, -0.0441$	stable
Complement	$\{x_1, x_2, x_3\}$	$-0.463, -0.1, -0.000905, -0.0208, -0.0201$	stable
709 Prey eco-evo	$\{B, x_1, x_2, x_3\}$	$0, -5.06 \cdot 10^{-8}, -0.0222, -0.0441$	neutrally stable
Complement	$\{S, P, x_4, x_5\}$	$0, -0.564, -0.0207, -0.0201$	neutrally stable
Predator evo	$\{x_4, x_5\}$	$-0.0208, -0.0201$	stable
Complement	$\{S, B, P, x_1, x_2, x_3\}$	$-0.463, -0.00436 \pm 0.0792i, -0.1, -0.0368, -0.0222$	stable
Predator eco-ev	$\{P, x_4, x_5\}$	$0, -0.0208, -0.0201$	neutrally stable
Complement	$\{S, B, x_1, x_2, x_3\}$	$-0.463, 0.102, -0.044, -0.0222, -5.01 \cdot 10^{-8}$	stable

## 710 S4.5 Haafke et al. (13) Model

The model is

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

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

716 The four ecological variables of the continuous trait model are nitrogen concentration  
 717 ( $N$ ), total algal density ( $A = A_1 + A_2$ ), and total breeding ( $R = R_1 + R_2$ ) and senes-  
 718 cent ( $S = S_1 + S_2$ ) rotifers. The evolutionary variables are  $x_1 = A_1/A$ ,  $x_2 = R_1/R$ ,  
 719 and  $x_3 = S_1/S$ . The equilibrium of the continuous trait model is  $(N, A, R, S, x_1, x_2, x_3) =$   
 720  $(22.7, 0.185, 5.9, 6.65, 0.5, 0.627, 0.627)$ . The Jacobian is

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

721 where the order of the columns and rows is  $(N, A, R, S, x_1, x_2, x_3)$ . The eigenvalues are  
 722  $(0.0156 \pm 0.369i, 0.0602 \pm 0.274i, -0.417 \pm 0.133i, -0.423)$ , which implies the equilibrium  
 723 is unstable. The instability of the equilibrium is due to a Hopf bifurcation that occurs at  
 724  $\delta \approx 0.734$ . The stabilities of the complementary pairs are given in Table S6.

725

726 **Table S6:** Stabilities of subsystems for the Haafke et al. (13) model

Subsystem	Variables	Eigenvalues	Stability
Ecological	$\{N, A, R, S\}$	$0.00149 \pm 0.387i, -0.418 \pm 0.136i$	unstable
Evolutionary	$\{x_1, x_2, x_3\}$	$0.0729 \pm 0.259i, -0.419$	unstable
Prey evo	$\{x_1\}$	0.0816	unstable
Complement	$\{N, A, R, S, x_2, x_3\}$	$0.00149 \pm 0.387i, -0.418 \pm 0.136i, -0.355, 0$	unstable
727 Prey eco-evo	$\{A, x_1\}$	0.134, 0.0694	unstable
Complement	$\{N, R, S, x_2, x_3\}$	0, 0, -0.599, -0.355, -0.355	neutrally stable
Predator evo	$\{x_2, x_3\}$	0, -0.355	neutrally stable
Complement	$\{N, A, R, S, x_1\}$	$-0.418 \pm 0.132i, 0.013 \pm 0.38i, 0.0595$	unstable
Predator eco-evo	$\{R, S, x_2, x_3\}$	0, 0, -0.355, -0.355	neutrally stable
Complement	$\{N, A, x_1\}$	$-0.244 \pm 0.212i, 0.0917$	unstable

## 728 S4.6 Hiltunen et al. (35) Model

The model is

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

729 where  $S$  is the concentration of limiting substrate,  $A_i$  is the density of algal clones ( $i = 1, 2$ ),  
 730  $R$  is the density of rotifers (the intraguild predator), and  $F$  is the density of flagellates (the  
 731 intraguild prey). In the model  $E_R = p_1 A_1 + p_2 A_2$  and  $E_F = \pi_1 A_1 + \pi_2 A_2$ . The three  
 732 parameterizations for figures 1b-d are listed below.

733 The four ecological variables of the continuous trait model are  $S$ ,  $A = A_1 + A_2$ ,  $R$ , and  $F$   
 734 and the evolutionary variable is  $x_1 = A_1/A$ . Note that the ecological subsystem  $\{S, A, R, F\}$   
 735 and the complementary evolutionary subsystem  $\{x_1\}$  also define the prey evolutionary sub-  
 736 system and its complement.

737

738 **Figure 1b:** The parameter values are  $\delta = 1$ ,  $r = 2$ ,  $k_1 = 0.234$ ,  $k_2 = 0.19$ ,  $p_1 = 0.05$ ,  $p_2 = 1$ ,  
 739  $g = 2$ ,  $k_r = 0.2$ ,  $\alpha_F = 0.05$ ,  $\pi_1 = 1$ ,  $\pi_2 = 0.1$ ,  $h = 3$ ,  $\eta = 0.08$ ,  $I_F = 0.001$ . The equilibrium  
 740 of the continuous trait model is  $(S, A, R, F, x_1) = (0.372, 0.497, 0.0608, 0.0711, 0.633)$ . The  
 741 Jacobian for the continuous trait model is

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

742 where the order of the columns and rows is  $(S, A, R, F, x)$ . The eigenvalues are  
743  $(-1, -0.29 \pm 0.506i, 0.0422 \pm 0.363i)$ , which implies the equilibrium is unstable. The insta-  
744 bility of the equilibrium is due to a Hopf bifurcation that occurs at  $\delta \approx 1.17$ . The stabilities  
745 of the complementary pairs are given in Table S7.

746

747 **Figure 1c:** The parameter values are  $\delta = 1$ ,  $r = 3.3$ ,  $k_1 = 0.1475$ ,  $k_2 = 0.07375$ ,  $p_1 = 0.05$ ,  
748  $p_2 = 1$ ,  $g = 2.5$ ,  $k_R = 0.2$ ,  $\alpha_F = 0.05$ ,  $\pi_1 = 1$ ,  $\pi_2 = 0.05$ ,  $h = 3$ ,  $\eta = 0.4$ ,  $I_F = 0.001$ . The  
749 equilibrium of the continuous trait model is  $(S, A, R, F, x_1) = (0.168, 0.456, 0.146, 0.231, 0.869)$ .  
750 The Jacobian for the continuous trait model is

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

751 where the order of the columns and rows is  $(S, A, R, F, x)$ . The eigenvalues are  
752  $(-1 \pm 1.12, -1, 0.0395 \pm 0.619i)$ , which implies the equilibrium is unstable. The instability  
753 of the equilibrium is due to a Hopf bifurcation that occurs at  $\delta \approx 1.69$ . The stabilities of the  
754 complementary pairs are given in Table S7.

755

756 **Figure 1d:** The parameter values are  $\delta = 1$ ,  $r = 2$ ,  $k_1 = 0.19$ ,  $k_2 = 0.12$ ,  $p_1 = 0.1$ ,  $p_2 = 1$ ,  
757  $g = 2$ ,  $k_R = 0.2$ ,  $\alpha_F = 0.05$ ,  $\pi_1 = 1$ ,  $\pi_2 = 1$ ,  $h = 3$ ,  $\eta = 0.4$ ,  $I_F = 0.001$ . The equilibrium  
758 of the continuous trait model is  $(S, A, R, F, x_1) = (0.485, 0.343, 0.03307748540, 0.14, 0.622)$ .  
759 The Jacobian for the continuous trait model is

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

760 where the order of the columns and rows is  $(S, A, R, F, x)$ . The eigenvalues are  
761  $(-1, -0.106 \pm 0.763i, 0.0052 \pm 0.174i)$ , which implies the equilibrium is unstable. The insta-  
762 bility of the equilibrium is due to a Hopf bifurcation that occurs at  $\delta \approx 1.17$ . The stabilities  
763 of the complementary pairs are given in Table S7.

764



765 **Table S7:** Stabilities of subsystems for the Hiltunen et al. (35) model

	Subsystem	Variables	Eigenvalues	Stability
<b>Fig. 1b</b>	Ecological	$\{N, C, B, S\}$	$-1, -0.285 \pm 0.503i, -0.00317$	stable
	Evolutionary	$\{x_1\}$	0.0786	unstable
	Prey eco-evo	$\{C, x_1\}$	$-6.32 \cdot 10^{-11}, 0.138$	unstable
	Complement	$\{N, B, S\}$	$-1.62, -0.00698 \pm 0.00395i$	stable
	Predator eco	$\{B, S\}$	$-0.00698 \pm 0.00395i$	stable
	Complement	$\{N, C, x_1\}$	$-0.784 \pm 0.283i, 0.0877$	unstable
<b>Fig. 1c</b>	Ecological	$\{N, C, B, S\}$	$-0.997 \pm 1.146i, -1, -0.129$	stable
	Evolutionary	$\{x_1\}$	0.202	unstable
	Prey eco-evo	$\{C, x_1\}$	$-1.93 \cdot 10^{-11}, 0.262$	unstable
	Complement	$\{N, B, S\}$	$-3.19, 0.00183 \pm 0.237i$	unstable
	Predator eco	$\{B, S\}$	$0.00183 \pm 0.237i$	unstable
	Complement	$\{N, C, x_1\}$	$-1.57 \pm 1.16i, 0.207$	unstable
<b>Fig. 1d</b>	Ecological	$\{N, C, B, S\}$	$-1, -0.11 \pm 0.764i, -0.0142$	stable
	Evolutionary	$\{x_1\}$	0.0337	unstable
	Prey eco-evo	$\{C, x_1\}$	$0.068, 1.34 \cdot 10^{-12}$	unstable
	Complement	$\{N, B, S\}$	$-1.263, -0.00322 \pm 0.0709i$	stable
	Predator eco	$\{B, S\}$	$-0.00322 \pm 0.0709i$	stable
	Complement	$\{N, C, x_1\}$	$-0.779, -0.46, 0.0395$	unstable

766

## 767 S4.7 Kasada et al. (26) Model

The model is

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

768 where  $N$  is concentration of nitrogen,  $C_i$  is the density of algal clones ( $i = 1, 2$ ), and  $B$   
 769 is the density of rotifers. We only focus on the parameter values for the UTEX396 and  
 770 UTEX265 algal clones because coexistence of multiple clonal types did not occur for other  
 771 combinations. This corresponds to figure 4E in Kasada et al. (26). The parameter values  
 772 are  $\beta_1 = 1.77$ ,  $\beta_2 = 1.57$ ,  $p_1 = 0.102$ ,  $p_2 = 0.102 \cdot 0.688$ ,  $N_I = 80$ ,  $\delta = 0.5$ ,  $\chi_c = 0.05$ ,  
 773  $\chi_b = 54000$ ,  $m = 0.055$ ,  $K_c = 4.3$ ,  $K_b = 0.835$ ,  $\omega_c = 20$ ,  $\varepsilon = 1$ ,  $G = 5 \cdot 10^{-5}$ .

774 For the continuous trait model the ecological variables are  $N$ ,  $C = C_1 + C_2$ , and  $B$  and  
 775 the evolutionary variable is  $x_1 = C_1/C$ . The equilibrium of the continuous trait model is  
 776  $(N, C, B, x_1) = (3.42, 2.63, 58500, 0.38)$ . The Jacobian for the system is

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

777 where the order of the columns and rows is  $(N, C, B, x)$ . The eigenvalues are  
 778  $(-5.99, -0.455, -0.239, -0.0117)$ , which implies the equilibrium is stable. The stabilities of  
 779 the complementary pairs are given in Table S8. Note that the ecological subsystem and the  
 780 complementary evolutionary subsystem also define the prey evolutionary subsystem and its  
 781 complement.

782 **Table S8:** Stabilities of subsystems for the Kasada et al. (26) model

Subsystem	Variables	Eigenvalues	Stability
Ecological	$\{N, C, B\}$	$-5.99, -0.455, -0.25$	stable
Evolutionary	$\{x_1\}$	0.00166	unstable
783 Prey eco-evo	$\{C, x_1\}$	$0.0487, -3.21 \cdot 10^{-11}$	stable
Complement	$\{N, B\}$	$0, -6.74$	neutrally stable
Predator eco	$\{B\}$	0	neutral
Complement	$\{N, C, x_1\}$	$-5.98, -0.709, 0.000837$	unstable

784 **S4.8 Wei et al. (34) Model**

The model is

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

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

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

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

792

793 **Figure 5a:** This parameterization assumes  $N$ ,  $X$ ,  $NW$ , and  $N_{12}$  are not present, i.e.,  
794 there are no bacteria susceptible to both or none of the phage types. The ecological vari-  
795 ables of the continuous trait model are the total densities of the different bacterial types  
796 and phage:  $\bar{N} = N_1 + N_2$ ,  $\bar{NW} = NW_1 + NW_2$ ,  $\bar{X} = X_1 + X_2$ , and  $\bar{P} = P_1 + P_2$ .  
797 To avoid notational confusion, we use  $\chi_i$  to denote the evolutionary traits. The evo-  
798 lutionary variables are  $\chi_1 = N_1/\bar{N}$ ,  $\chi_2 = NW_2/\bar{NW}$ ,  $\chi_3 = X_1/\bar{X}$ , and  $\chi_4 = P_1/\bar{P}$ .  
799 The equilibrium is  $(R, \bar{N}, \bar{NW}, \bar{X}, \bar{P}, \chi_1, \chi_2, \chi_3, \chi_4) = (94.6, 4.87 \cdot 10^6, 3.25 \cdot 10^6, 1210, 5.36 \cdot$   
800  $10^6, 0.832, 0.832, 0.832, 0.0824)$ . The Jacobian for the system is

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

801 where the order of the columns and rows is  $(R, \bar{N}, \bar{N}\bar{W}, \bar{X}, \bar{P}, \chi_1, \chi_2, \chi_3, \chi_4)$ . The eigenvalues  
802 are  $(-0.0017 \pm 0.443i, -0.00167 \pm 0.42i, -0.015, -0.015, -0.4, -0.4, -0.4)$ , which implies the  
803 equilibrium is stable. The stabilities of the complementary pairs are given in Table S9.

804 **Table S9:** Stabilities of subsystems for the Fig. 5a Wei et al. (34) model

Subsystem	Variables	Eigenvalues	Stability
Ecological	$\{R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}\}$	$-0.0017 \pm 0.439i, -0.015, -0.4, -0.4$	stable
Evolutionary	$\{x_1, x_2, x_3, x_4\}$	$-0.00166 \pm 0.421i, -0.4, -0.015$	stable
Prey evo	$\{x_1, x_2, x_3\}$	$-0.4, -5.22 \cdot 10^{-21}, -0.0183$	stable
Complement	$\{R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}, x_4\}$	$-0.0017 \pm 0.439i, -0.015, -0.4, -0.4, 0$	neutrally stable
805 Prey eco-evo	$\{\bar{N}, N\bar{W}, \bar{X}, x_1, x_2, x_3\}$	$-5 \cdot 10^{-21}, -0.0183, -0.4, -0.4, -5.23 \cdot 10^{-21}, -0.0183$	stable
Complement	$\{R, \bar{P}, x_4\}$	$0, 0, -0.4$	neutrally stable
Predator evo	$\{x_4\}$	$0$	neutral
Complement	$\{R, \bar{N}, N\bar{W}, \bar{X}, \bar{P}, x_1, x_2, x_3\}$	$-0.0017 \pm 0.441i, -4 \cdot 10^{-7}, -0.015, -0.0183, -0.4, -0.4, -0.4$	stable
Predator eco-evo	$\{\bar{P}, x_4\}$	$0, 0$	neutral
Complement	$\{R, \bar{N}, N\bar{W}, \bar{X}, x_1, x_2, x_3\}$	$-0.00008, -0.0184, -0.4, -0.4, -0.4, -7.29 \cdot 10^{-24}, -0.0183$	stable

806 **Figure 5b:** This parameterization assumes  $N_2$ ,  $X_2$  and  $NW_2$  are not present, i.e.,  
 807 there are no types that are just resistant to phage 2. For the continuous trait model  
 808 the ecological variables are the total densities of the different bacterial types and phage:  
 809  $\bar{N} = N + N_1 + N_{12}$ ,  $\bar{NW} = NW + NW_1$ ,  $\bar{X} = X + X_1$ , and  $\bar{P} = P_1 + P_2$ . To avoid  
 810 notational confusion, we use  $\chi_i$  to denote the evolutionary traits. The evolutionary vari-  
 811 ables are  $\chi_1 = N_1/\bar{N}$ ,  $\chi_2 = N_{12}/\bar{N}$ ,  $\chi_3 = NW/\bar{NW}$ ,  $\chi_4 = X/\bar{X}$ , and  $\chi_5 = P_1/\bar{P}$ .  
 812 The equilibrium is  $(R, \bar{N}, \bar{NW}, \bar{X}, \bar{P}, \chi_1, \chi_4, \chi_2, \chi_3, \chi_5) = (.25, 1.98 \cdot 10^8, 4.8 \cdot 10^6, 901, 6.44 \cdot$   
 813  $10^7, 0.029, 0.964, 0.203, 0.203, 0.104)$ . The Jacobian for the system is

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

814 where the order of the columns and rows is  $(R, \bar{N}, \bar{NW}, \bar{X}, \bar{P}, \chi_1, \chi_4, \chi_2, \chi_3, \chi_5)$ . The eigen-  
 815 values are  $(-79.8, -0.00198 \pm 0.162i, -0.00168 \pm 0.1i, -0.015, -0.0151, -0.401, -0.4 - 0.4i)$ ,  
 816 which implies the equilibrium is stable. The stabilities of the complementary pairs are given  
 817 in Table S10.



818 **Table S10:** Stabilities of subsystems for the Fig. 5b Wei et al. (34) model

Subsystem	Variables	Eigenvalues	Stability
Ecological	$\{R, \bar{N}, \bar{N}W, \bar{X}, \bar{P}\}$	$-79.8, -0.000645, -0.015, -0.401, -0.4$	stable
Evolutionary	$\{x_1, x_2, x_3, x_4, x_5\}$	$-0.4, -0.00164 \pm 0.119i, -0.00321, -0.015$	stable
Prey evo	$\{x_1, x_2, x_3, x_4\}$	$-0.4, -0.0183, -1.88 \cdot 10^{-18}, -0.00321$	stable
Complement	$\{R, \bar{N}, \bar{N}W, \bar{X}, \bar{P}, x_5\}$	$-79.8, -0.401, -0.4, -0.015, -0.000645, 3.57 \cdot 10^{-15}$	unstable
Prey eco-evo	$\{\bar{N}, \bar{N}W, \bar{X}, x_1, x_2, x_3, x_4\}$	$1.6 \cdot 10^{-20}, -0.0183, -0.4, -0.0183$ $-0.4, 8.67 \cdot 10^{-20}, 9.31 \cdot 10^{-20}$	unstable
819 Complement	$\{R, \bar{P}, x_5\}$	$0, 0, -80.2$	neutrally stable
Predator evo	$\{x_5\}$	$0$	neutral
Complement	$\{R, \bar{N}, \bar{N}W, \bar{X}, \bar{P}, x_1, x_2, x_3, x_4\}$	$-79.8, -0.00202 \pm 0.148i, -0.401, -0.4$ $-0.4, -0.0183, -0.015, 3.54 \cdot 10^{-16}$	stable
Predator eco-evo	$\{\bar{P}, x_5\}$	$0, 0$	neutral
Complement	$\{R, \bar{N}, \bar{N}W, \bar{X}, x_1, x_2, x_3, x_4\}$	$-79.8, -0.0182, -0.402, -0.4$ $-0.4, -0.0183, -8.42 \cdot 10^{-20}, 3.02 \cdot 10^{-18}$	unstable

## 820 S4.9 Yoshida et al. (10; 11) Model

The model is

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

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

826 For the continuous trait model the ecological variables are  $N$ ,  $C = C_1 + C_2$ ,  $B$ , and  $R$   
 827 and the evolutionary variable is  $x_1 = C_1/C$ . The equilibrium of the continuous trait model  
 828 is  $(N, C, B, R, x_1) = (0.731, 1.07, 690, 449, 0.495)$ . The Jacobian for the system is

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

829 where the order of the columns and rows is  $(N, C, B, R, x_1)$ . The eigenvalues are  
 830  $(-17.8, -0.864, -0.562, 0.0028 \pm 0.219i)$ , which implies the equilibrium is unstable. The  
 831 instability of the equilibrium is due to a Hopf bifurcation that occurs at  $\delta \approx 0.7$ . The  
 832 stabilities of the complementary pairs are given in Table S11.

833 **Table S11:** Stabilities of subsystems for the Yoshida et al. (10; 11) model

Subsystem	Variables	Eigenvalues	Stability
Ecological	$\{N, C, B, R\}$	$-17.9, -0.0951, -0.535, -0.856$	stable
Evolutionary	$\{x_1\}$	0.079	unstable
Prey evo	$\{x_1\}$	0.079	unstable
834 Complement	$\{N, C, B, R\}$	$-17.9, -0.0951, -0.535, -0.856$	stable
Prey eco-evo	$\{C, x_1\}$	$0.167, 1.43 \cdot 10^{-10}$	unstable
Complement	$\{N, B, R\}$	$-18.7, -0.745, 0$	neutrally stable
Predator eco	$\{B, R\}$	$0, -0.745$	neutrally stable
Complement	$\{N, C, x_1\}$	$-17.8, -0.741, 0.0659$	unstable