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A mutualism–parasitism continuum model and its application to plant–mycorrhizae interactions

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Abstract

We consider interactions between a symbiont and its host in the framework of the familiar Lotka–Volterra predator–prey model, modified to allow the symbiont to benefit the host. The model includes both benefits and costs to the interaction and spans the mutualism–parasitism continuum. We use this model to explore the shift from mutualism to parasitism in plant–mycorrhizae interactions across gradients of soil fertility. We demonstrate two mechanisms by which increased soil fertility may cause interactions to change from mutualistic to parasitic: as relative benefits to the plant decrease with increasing soil fertility, the interaction between the fungus and its host turns parasitic; with two fungal species—one a mutualist and the other a cheater—increasing soil fertility can favor the cheater if mutualists have faster growth rates than cheaters.

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1. Introduction

Mutualistic interactions, although ubiquitous in nature, are not well understood theoretically (Boucher, 1985; Herre et al., 1999; Hoeksema and Bruna, 2000). A variety of theoretical approaches have been developed to model mutualisms (reviewed in Hoeksema and Bruna, 2000), including the iterated prisoner's dilemma and other game theoretic approaches, biological market models, and models for the evolution of virulence. There have been a number of recent articles that use different approaches

to modeling mutualisms, mutualist/exploiter coexistence (Johnstone and Bshary, 2002; Morris et al., 2003; Wilson et al., 2003), and conditions favoring mutualism (Hoeksema and Schwartz, 2002; Nuismer et al., 2003). Relatively lacking, however, have been Lotka–Volterra type models, which are frequently used by ecologists to study competition and predator–prey interactions. This may stem from the impression that such models when applied to mutualistic interactions are not generally stable (May (1974): “mutualism between species tends to have a destabilizing effect on the community dynamics”). Indeed, simple Lotka–Volterra mutualism models often predict that both species increase to populations of infinite size.

However, incorporation of nonlinearities (e.g. density dependence) into Lotka–Volterra mutualism models for either the host or the symbiont often results in stable equilibria (Whittaker, 1975; Vandermeer and Boucher, 1978; May, 1981; Soberon and Martinez del

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Rio, 1981; Wells, 1983; Vandermeer and Goldberg, 2003, p. 238; Zhang, 2003). Similarly, including a spatial component stabilizes the interaction (Tainaka et al., 2003). These modified models have been applied to a variety of ecological interactions, such as plant–pollinator interactions (Soberon and Martinez del Rio, 1981; Wells, 1983; Holland et al., 2002) and legume–rhizobium interactions (Vandermeer and Boucher, 1978; Simms and Taylor, 2002; West et al., 2002).

Researchers have recognized that symbiotic interactions may shift between mutualism and parasitism, depending on endogenous or exogenous factors (Thompson, 1988; Bronstein, 1994; Herre et al., 1999; Hernandez, 1998; Johnson et al., 2003). However, traditional mutualism models do not include the possibility of negative effects between species, nor do traditional predator–prey models include the possibility of positive effects of the predator species on the prey species. Thus, neither type of model can explore shifts between mutualism and parasitism. We modify a Lotka–Volterra model to include both positive and negative effects between species and show how it can be applied to mutualism–parasitism shifts. Specifically, we address the questions (1) what factors determine whether a species behaves as a mutualist or a parasite? and (2) what factors control the outcome of competition between a cheater and a mutualist? The framework of the Lotka–Volterra model has the benefits of being widely familiar to ecologists and of explicitly quantifying population densities (unlike many game theoretical or biological market models).

2. The model

We adopt the view that mutualistic interactions are essentially exploitative where one species exploits the other to gain a benefit (Herre et al., 1999), and thus both costs and benefits must be taken into account to successfully model mutualisms (Holland et al., 2002). The model we propose is based on the classical predator–prey/host–parasite Lotka–Volterra model with the additional possibility of the parasite benefiting the host. It is this mechanism that might turn the interaction mutualistic. We retain the notation of the host–parasite model, but refer to the parasite as the symbiont because it may operate as either a

mutualist or a parasite. We make the following model assumptions: (1) the host dynamics in the absence of the symbiont follow logistic growth; (2) the symbiont has both a positive and a negative effect on the host: the presence of the symbiont benefits the host by increasing the host's carrying capacity, but also results in an increased death rate of the host due to exploitation; (3) self-interference of the symbiont increases the symbiont's death rate. These assumptions result in the following model equations:

$$\begin{aligned}\frac{dH}{dt} &= rH \left(1 - \frac{H}{K + \gamma P} \right) - aHP \\ \frac{dP}{dt} &= bHP - dP(1 + eP)\end{aligned}\quad (1)$$

where H denotes the density of the host and P the density of the symbiont. All parameters in the model are assumed to be positive, except for γ , which is assumed to be nonnegative. The parameter K is the carrying capacity; the parameter r is the intrinsic rate of growth of the host; the parameter a represents the exploitation of the host by the symbiont, which leads to a reduction in the growth rate of the host. The parameter b is the growth rate of the symbiont. The parameters d and e describe the symbiont's density independent and dependent death rates, respectively. The term γP incorporates the gain to the host from the interaction with the symbiont. When $\gamma = 0$, the model reduces to a modified Lotka–Volterra predator–prey model that includes density dependence for the host and the symbiont (i.e. the terms in the parentheses). Incorporating density dependence for the host population is sufficient to stabilize the coexistence equilibrium (if it exists).

We chose this particular model, which includes symbiont density dependence, because it can be extended to include competition between multiple symbionts in a model framework analogous to Lotka–Volterra competition models. We analyze the two species model first before discussing competition between multiple symbionts. We assume $K > d/b$. In biological terms, this means that the host carrying capacity in absence of the symbiont can support positive symbiont growth so that a symbiont can invade an equilibrial host population. This seems biologically realistic and simplifies the analysis.

There are two distinct methods to characterize an equilibrium as either mutualistic or parasitic. These

have empirical and analytical analogues (Bender et al., 1984). The first method can be described as a long-term equilibrium approach: The host is grown in both the presence and the absence of the symbiont until equilibria are reached (i.e. a control and a symbiont treatment). The interaction is characterized as mutualistic if the host biomass is larger in the presence of the symbiont than when the symbiont is absent and parasitic otherwise. The direct mathematical analogue is to compare the host monoculture equilibrium in which the symbiont is absent to the host equilibrium density of the nontrivial equilibrium in which both host and symbiont are present. The second method can be described as a pulse experiment approach (Bender et al., 1984): host and symbiont are grown together until they reach equilibrium. If increasing symbiont density (simply by adding symbionts) increases the growth rate of the host, the interaction is characterized as mutualistic, otherwise as parasitic. The two types of experiments (and likewise their mathematical counterparts) do not necessarily yield the same characterization (Bender et al., 1984).

The mathematical analogue of the pulse experiment is based on standard graphical phase plane analysis. It utilizes the sign structure of the Jacobian matrix, denoted by J , evaluated at the equilibrium (May, 1974).

We are particularly interested in nontrivial equilibria, that is, equilibria in which the densities of both host and symbiont are positive. A nontrivial equilibrium occurs when the two zero isoclines cross in the first quadrant (Fig. 1). Under the assumption $K > d/b$, there exists exactly one such point. To find the signs in the Jacobian matrix, we determine how dH/dt and dP/dt change as either H or P increases. For instance, to find the first entry in the Jacobian matrix ($\partial(dH/dt)/\partial H$), we move along a horizontal line through the equilibrium point in the direction of increasing host density. Since we move from a region where dH/dt is positive to a region where dH/dt is negative, dH/dt decreases as H increases and thus $\partial(dH/dt)/\partial H < 0$. The other entries can be found similarly.

Whether the interaction is parasitic or mutualistic (sensu May, 1974) depends upon whether the joint equilibrium occurs above or below the vertex. When the symbiont isocline crosses the host isocline below the vertex (Fig. 1: isocline 1), the Jacobian matrix is of the form $\begin{bmatrix} - & + \\ + & - \end{bmatrix}$ and the interaction is mutualistic in the sense that an increase in symbiont density has a positive effect on the growth rate of the host at equilibrium (the entry $\partial(dH/dt)/\partial P$ is positive). When the symbiont isocline crosses the host isocline above the

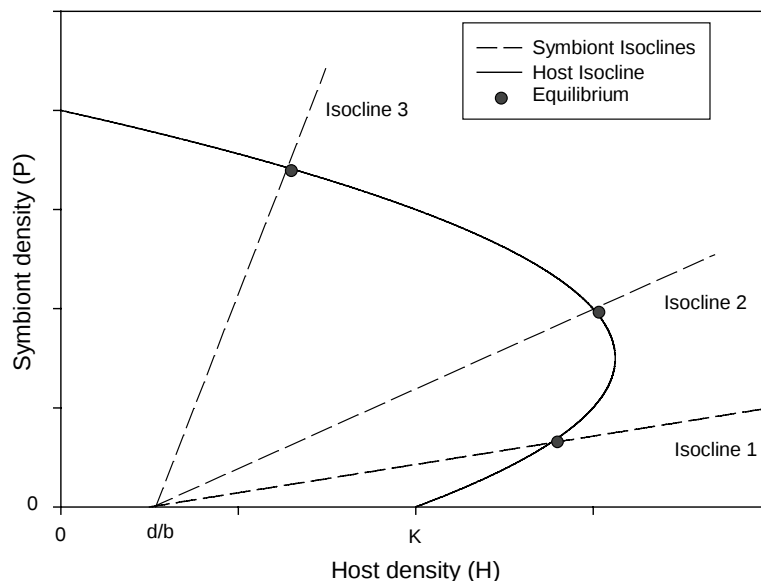


Fig. 1. If $K > d/b$, the two isoclines intersect in the first quadrant and a (unique) nontrivial equilibrium exists. The three symbiont isoclines illustrate the different outcomes of the interactions.

vertex (Fig. 1: isoclines 2 and 3), the Jacobian matrix is of the form $\begin{bmatrix} - & - \\ + & - \end{bmatrix}$ and the interaction is parasitic in the sense that an increase in symbiont density has a negative effect on the growth rate of the host at equilibrium (the entry $\partial(dH/dt)/\partial P$ is negative). If the vertex is below the x-axis (in the fourth quadrant), then it is impossible for the joint equilibrium to be below the vertex, and the interaction is always parasitic. This occurs when the second coordinate of the vertex is negative. The coordinates of the vertex are given by $(K/2 + \gamma r/4a + aK^2/4r\gamma, r/2a - K/2\gamma)$, so the interaction is always parasitic when $K > \gamma r/a$. Thus, in this model as in nature, interactions between two species can range from mutualistic to parasitic (Thompson, 1988; Bronstein, 1994; Herre et al., 1999).

Oscillations, which are common in host parasite interactions, are not a feature of the mutualistic interactions in this two-species model. When the interaction is characterized as mutualistic based on the Jacobian matrix, the equilibrium is a nodal sink (eigenvalues are real and negative; the equilibrium is approached via exponential decay). As the interaction turns more parasitic, a qualitative shift occurs from a nodal sink to a spiral sink (eigenvalues are complex with negative real parts; the equilibrium is approached via damped oscillations). To determine where eigenvalues are real, it is sufficient that $\text{Tr}(J)^2 - 4\det(J) > 0$, where $\text{Tr}(J)$ is the trace and $\det(J)$ the determinant of the Jacobian matrix. If $J = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$, then $\text{Tr}(J)^2 - 4\det(J) = (a_{11} - a_{22})^2 + 4a_{12}a_{21} > 0$ if both a_{12} and a_{21} are positive, as is the case if the interaction is mutualistic. Thus, all mutualistic interactions have a nodal sink. Parasitic interactions may have either a nodal sink or a spiral sink: as the interaction becomes more parasitic, the equilibrium point shifts from a nodal sink to a spiral sink.

Note that isocline 2 in Fig. 1 results in an equilibrium that is characterized as being parasitic based on the Jacobian matrix (at equilibrium, increases in symbiont abundance decrease host growth), even though the host equilibrium density is higher in the presence of the symbiont than when the symbiont is absent and would thus be characterized as mutualistic based on the long-term equilibrium approach. Isocline 3 (Fig. 1) would be characterized as parasitic by

both the Jacobian matrix and equilibrium abundances approaches. The fact that the characterization of equilibria as mutualistic or parasitic based on the Jacobian matrix does not always agree with the characterization based on equilibrium densities is perhaps not surprising, as the Jacobian matrix analysis refers to the transient dynamics following a small perturbation and is thus a local analysis (see Neubert et al., 2002, for instance, for a discussion of this approach), whereas the comparison of equilibria is a global feature, not reflected by the Jacobian matrix. Both characterizations, however, are important since both have experimental analogues. We subsequently explore both the use of the Jacobian matrix and the criterion of increased host abundance in the presence of the symbiont to determine whether interactions are mutualistic or parasitic. To avoid redundancy, we defer further discussion of the factors controlling the mutualism parasitism shift to the plant–mycorrhizae application discussed below. We note that our analysis relies on the shape of the isoclines and not on their precise analytical form. Qualitatively similar results thus occur for other models with qualitatively similar zero isoclines.

In nature, most mutualisms involve multiple species on both sides of the interaction (Horvitz and Schemske, 1990; Thompson and Pellmyr, 1992; Pellmyr and Thompson, 1996), raising the question of how species that share a mutualist coexist. In addition, many mutualist species may share a host with parasitic species, which also begs the question of coexistence (Denison, 2000; Morris et al., 2003). To address this latter question, we include a second symbiont whose density is denoted by Q . We assume that the second symbiont is a cheater, that is, it does not confer any benefits to the plants. Because the symbiont P has the potential to act as a mutualist, we will refer to species P and Q as mutualist and cheater, respectively. The interaction between the two species is modeled analogously to classical competition, where

$$\begin{aligned} \frac{dH}{dt} &= rH \left(1 - \frac{H}{K + \gamma P} \right) - a_1 PH - a_2 QH \\ \frac{dP}{dt} &= b_1 HP - d_1 P(1 + e_1 P + c_1 Q) \\ \frac{dQ}{dt} &= b_2 HQ - d_2 Q(1 + e_2 Q + c_2 P) \end{aligned} \quad (2)$$

All parameters, except for c_1 , c_2 , and γ are positive. The parameters c_1 , c_2 , and γ are nonnegative. The interpretation of the parameters in these equations is the same as in the single symbiont case, with the addition of interspecific competition terms to the symbiont equations. The strength of interspecific competition is measured by the parameters c_1 and c_2 . As before, we assume $K > (d_1/b_1), (d_2/b_2)$. Furthermore, we assume $(b_1/d_1) > (b_2/d_2)$.

The three-species system has multiple equilibria. There is the trivial equilibrium $(0, 0, 0)$, which is always unstable. Furthermore, there are two *boundary equilibria* where one or the other symbiont is absent (as in our the two-species model), denoted by $(\bar{H}^{\bar{P}}, \bar{P}, 0)$ and $(\bar{H}^{\bar{Q}}, 0, \bar{Q})$, respectively, where $\bar{H}^{\bar{P}} > 0$ with $\bar{P} = (1/e_1)((b_1/d_1)\bar{H}^{\bar{P}} - 1) > 0$, and $\bar{H}^{\bar{Q}} > 0$ with $\bar{Q} = (1/e_2)((b_2/d_2)\bar{H}^{\bar{Q}} - 1) > 0$. The behavior of this three-species system can be conveniently summarized in terms of the competition coefficients c_1 and c_2 . Details are provided in [Appendix A](#). We define

$$\lambda_1^P = \frac{1}{e_1} \left(\frac{b_1}{d_1} \bar{H}^{\bar{P}} - 1 \right) \quad \text{and} \\ \lambda_2^P = \frac{1}{e_2} \left(\frac{b_2}{d_2} \bar{H}^{\bar{P}} - 1 \right)$$

and

$$\lambda_1^Q = \frac{1}{e_1} \left(\frac{b_1}{d_1} \bar{H}^{\bar{Q}} - 1 \right) \quad \text{and} \\ \lambda_2^Q = \frac{1}{e_2} \left(\frac{b_2}{d_2} \bar{H}^{\bar{Q}} - 1 \right).$$

λ gives the carrying capacity of a symbiont for a fixed host density (fixed at either $\bar{H}^{\bar{Q}}$ or $\bar{H}^{\bar{P}}$). The superscripts indicate the value used for host density, and the subscripts indicate whether λ is the carrying capacity of symbiont 1 (the mutualist) or 2 (the cheater). P can invade the $(\bar{H}^{\bar{Q}}, 0, \bar{Q})$ equilibrium if and only if

$$c_1 < e_1 \frac{\lambda_1^Q}{\lambda_2^Q}$$

and Q can invade the $(\bar{H}^{\bar{P}}, \bar{P}, 0)$ equilibrium if and only if

$$c_2 < e_2 \frac{\lambda_2^P}{\lambda_1^P}$$

This invasibility criterion tells us something about the stability of the boundary equilibria $(\bar{H}^{\bar{P}}, \bar{P}, 0)$ and $(\bar{H}^{\bar{Q}}, 0, \bar{Q})$ ([Fig. 2](#)). A further analysis is needed to

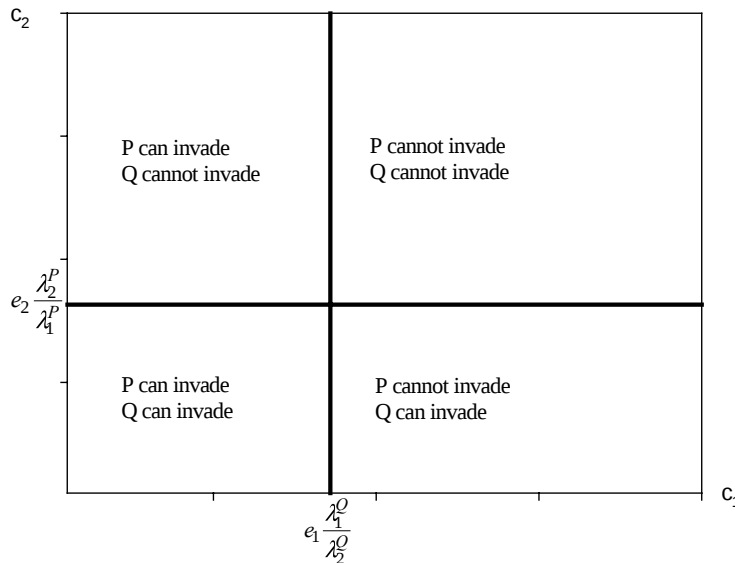


Fig. 2. The c_1 – c_2 plane is divided into four regions based on whether the mutualist or the cheater can invade.

determine the existence and stability of nontrivial equilibria (H^* , P^* , Q^*) with H^* , P^* , Q^* > 0.

We show in Appendix A that the equilibria $\bar{H}^P$, $\bar{P}$, $\bar{H}^Q$ and $\bar{Q}$ are increasing functions of the carrying capacity K , that these equilibria have finite limits as $K \rightarrow \infty$, and that if $(b_1/d_1) > (b_2/d_2)$, then $e_1(\lambda_1^Q/\lambda_2^Q)$ is a decreasing function of K and $e_2(\lambda_2^P/\lambda_1^P)$ is an increasing function of K .

Finding nontrivial equilibria and analyzing stability is algebraically quite involved. Based on geometric considerations, however, we can say the following (see Appendix A): there exists at most one nontrivial equilibrium if $c_1 < e_2(b_1/d_1)(d_2/b_2)$ and $c_2 < e_1(b_2/d_2)(d_1/b_1)$; if $c_1 < e_2(b_1/d_1)(d_2/b_2)$ and $c_2 > e_1(b_2/d_2)(d_1/b_1)$, there exists no nontrivial equilibrium; if $c_1 > e_2(b_1/d_1)(d_2/b_2)$, there may exist up to two nontrivial equilibria. Below, where we discuss shifts from mutualism to parasitism, we will provide numerical examples that illustrate the behavior of this three-species model.

3. An application: plant–mycorrhizae interactions

This model can be applied to plant–mycorrhizae interactions, where the plant represents the host and the fungus represents the parasite, reflecting our view that plant–mycorrhizae interactions are in essence exploitative. In this context, the most appropriate way to think about the population densities in the equations are in terms of biomass rather than in terms of numbers of individuals. The number of individuals in a mycorrhizae population is not empirically measurable. Also, the population sizes of these species may change at dramatically different rates, but because of the modular growth forms of both species, biomass responses may operate on a much more similar time scale.

The interaction between the fungus and its host plant consists of nutrient transfer: the plant provides the fungus with carbon compounds; the fungus delivers nutrients, such as phosphorus, to the plant. A plant may benefit from an infection with mycorrhizal fungi, particularly in soils with low availability of phosphorus. Carbon transfer from plant to fungus may decrease plant fitness, whereas nutrient transfer from fungus to plant may increase plant fitness (Smith and Read, 1997). However, the net benefit a fungus confers

to a plant declines with soil fertility, and may be negative in very fertile soils (Bowen, 1980; Johnson, 1993; Johnson et al., 1997; Saikkonen et al., 1998; Cairney and Meharg, 1999; Egerton-Warburton and Allen, 2000). Based on our model, we demonstrate two mechanisms by which increased soil fertility may cause interactions to change from mutualistic to parasitic: as relative benefits to the plant decrease with increasing soil fertility, the interaction between the fungus and its host turns parasitic; with two fungal species, a mutualist and a cheater, increasing soil fertility can favor the cheater.

Using the single host/single symbiont model, we demonstrate that an increase in soil fertility can turn a mutualistic relationship into a parasitic relationship. The change from mutualism to parasitism occurs because, as the limiting resource becomes more abundant, the relative benefit of the mycorrhizae supplying that resource is decreased. The effect of soil fertility can be studied by changing the carrying capacity K , which increases with soil fertility. As K increases while all other parameters are kept fixed, the vertex of the zero isocline of the host moves to the right and down (the dotted line in panel 1 in Fig. 3 indicates the location of the vertex as a function of K) implying that when K increases, a mutualistic relationship can change into a parasitic one. This can also be seen analytically from the coordinates of the vertex given by $(K/2 + \gamma r/4a + aK^2/4r\gamma, r/2a - K/2\gamma)$. An increase in K increases the first and decreases the second coordinate, thus changing the relative position of the equilibrium and the vertex of the host isocline. Using the pulse criterion, if the symbiont isocline (dashed lines in Fig. 3) intersects the host isocline below the vertex the interaction is mutualistic; if the intersection occurs below the vertex it is parasitic. The equilibrium abundance criterion also shows a shift from mutualism to parasitism with increasing host carrying capacity, such that for high values of host carrying capacity, the presence of the symbiont decreases host abundance. Although both criteria detect a switch from mutualism to parasitism, the shift from mutualism to parasitism based on the pulse criterion always occurs at a lower host carrying capacity than does the shift based on the equilibrium abundance criterion.

The amount of benefit the symbiont provides to the host (γ) also influences whether an interaction is mutualistic or parasitic. Using the pulse criterion, the

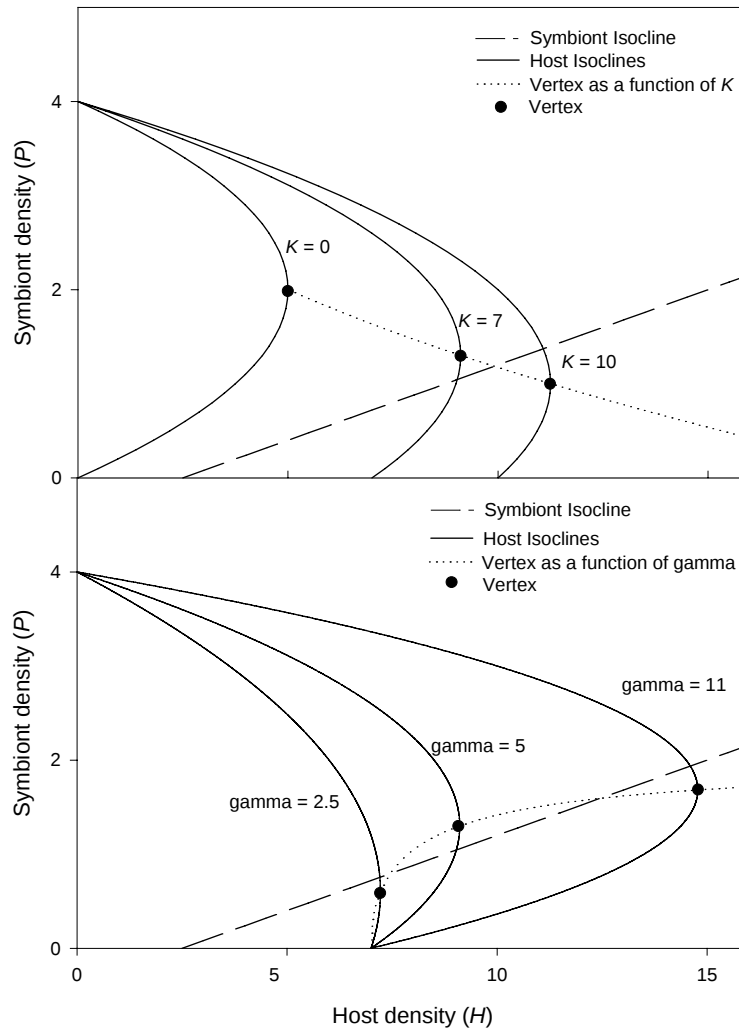


Fig. 3. Increased host carrying capacity (K) can change an interaction from mutualistic to parasitic. Increases in symbiont benefit (γ) can change an interaction from mutualistic to parasitic, and depending on the criterion used, back to parasitic. The fungus isocline is independent of K and γ , and intercepts H at d/b . The plant isocline is a sideways parabola. The location of the vertex is dependent on K and γ , with coordinates $(K/2 + \gamma r/4a + aK^2/4r\gamma, r/2a - K/2\gamma)$.

qualitative behavior of the equilibrium as a function of γ depends on the slope of the symbiont isocline. If the slope is too steep, the interaction is always parasitic. If not, the interaction is mutualistic for intermediate values of γ but parasitic for small or large values of γ (see panel 2 in Fig. 3). That the interaction is parasitic for small values of γ is not surprising since in this case the interaction reduces to an exploiter–victim relationship where the victim (that is the host) does not benefit from the presence of the exploiter (that is the

symbiont). As γ increases, the net benefit to the host can become positive. Surprisingly, a further increase in the benefit to the host can turn the interaction parasitic again. Because the benefit of the symbiont in our model occurs via increases in host carrying capacity, the host, as γ tends to infinity, becomes unlimited by carrying capacity, and is limited only by the negative effects of the symbiont. Thus, the equilibrium values approach those of a system where the host dynamics are described by the classical predator–prey

model ($dH/dt = rH - aHP$). The above discussion is based on pulse analyses. Based on the equilibrium abundance criterion, increases in γ always make the interaction more mutualistic. Note that the interaction depicted with $\gamma = 11$ (panel 2, Fig. 3) would be characterized as parasitic based on the pulse criterion, but mutualistic based on the equilibrium abundance criterion.

In nature, a single plant is often infected by more than one fungus (e.g. Helgason et al., 1998; Horton and Bruns, 1998; Allen et al., 1995). These fungi may range from mutualistic to parasitic, and may compete with each other (Wu et al., 1999). Using the single-host/two-symbiont model, we ask what happens when two fungi compete for the same host, and what controls the outcome of competition? Specifically, does an increase in soil fertility affect the outcome of competition? We use K as a measure for soil fertility. We consider the case of $(b_1/d_1) > (b_2/d_2)$, i.e., the mutualist grows faster than the cheater. This could occur, for instance, if the host rewards the mutualist more than the cheater by regulating the amount of carbon it transfers to the fungus. With these assumptions and fixed values of c_1 and c_2 , the outcome of competition shifts predictably with soil fertility. Specifically, we will demonstrate that it is possible to choose parameter values so that for small values of K only the mutualist and the host can coexist, but as K increases, the cheater becomes more and more favored

and will eventually be able to invade. The cheater will then either be able to coexist with the mutualist or even outcompete the mutualist, depending on the choice of parameters.

We use stability of boundary equilibria (i.e. whether mutualist or cheater can invade in the presence of the other) and the geometric shape of the isoclines to determine whether the mutualist and cheater can coexist or whether one is outcompeted by the other. Fig. 4 illustrates how changes in K affect the stability of the boundary equilibria for fixed values of c_1 and c_2 . It is thus possible to choose parameter values so that the cheater cannot invade the host-mutualist equilibrium for small values of K , but as K increases, either both the cheater and the mutualist will be able to invade or the cheater will be able to invade but the mutualist will not. This indicates that a switch from mutualism to parasitism can occur in this system as soil fertility increases.

We illustrate this switch using two examples with specific parameters. (Mathematical details can be found in Appendix A.) In the first example (see Table 1, Fig. 4, and Appendix A), the parameters c_1 and c_2 are chosen so that for small values of K , the mutualist can invade but the cheater cannot. As K increases, both mutualist and cheater can invade. Thus increasing carrying capacity (e.g. through fertilization) can cause the community to shift from mutualists only to mutualists and parasites.

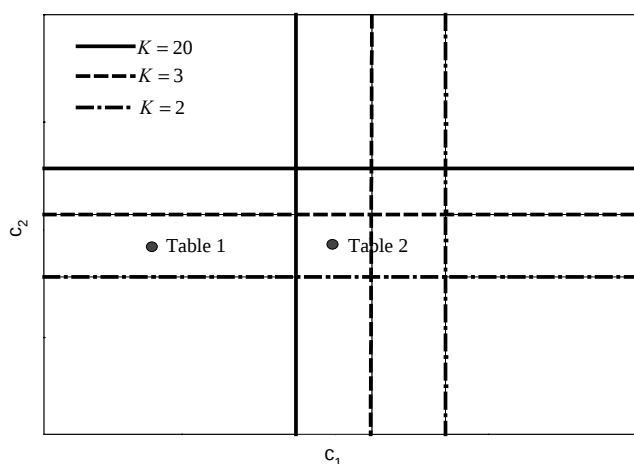


Fig. 4. For each of the three values of K , the lines $e_1(\lambda_1^Q/\lambda_2^Q)$ (vertical lines) and $e_2(\lambda_2^P/\lambda_1^P)$ (horizontal lines) are drawn that partition the c_1 – c_2 plane according to the behavior of the boundary equilibria. The locations of the dots indicate the choices of parameters for the simulations in Tables 1 and 2, respectively.

Table 1
The equilibria (H , P , Q) are listed together with their stability

H	P	Q	Stability
$K = 2$, P wins			
2.3939	6.1817	0	Locally stable
1.333	0	1.6667	Unstable
$K = 3$, coexistence			
2.3987	6.1961	0	Unstable
1.6364	0	2.2727	Unstable
2.3987	6.1918	0.030	Locally stable
$K = 20$, coexistence			
2.4503	6.3510	0	Unstable
2.6667	0	4.3333	Unstable
2.4508	6.2652	0.0623	Locally stable

Parameter values: $\gamma = 5$, $r = 2$, $a_1 = 0.3$, $a_2 = 0.4$, $b_1 = 3$, $b_2 = 2$, $c_1 = 1.400$, $c_2 = 0.6128$, $d_1 = 1$, $d_2 = 1$, $e_1 = 1$, $e_2 = 1$.

In the second example (see Table 2, Fig. 4, and Appendix A), the parameters c_1 and c_2 are chosen so that for small values of K , the mutualist can invade but the cheater cannot; for intermediate values of K , both can invade; for large values of K , the cheater can invade but the mutualist cannot. Thus, both examples illustrate a shift in the symbiont community from mutualist to cheater.

In addition, this set of parameter values results in multiple, locally stable equilibria at low values of K . Although the “mutualist-only” boundary equilibrium

is locally stable, there is an additional locally stable equilibrium point in which the mutualist and the cheater coexist. The existence of these two locally stable equilibria at low K means that although the cheater cannot successfully invade when present at low abundance, once present at sufficiently high abundance the mutualist and the cheater can coexist. This occurs when a highly beneficial mutualist, in the absence of the cheater, causes a high host and mutualist densities, and a high mutualist density competitively inhibits the growth of the cheater. When cheater density is higher, the density of mutualists is reduced, due both to direct competitive effects, and to the indirect effects of reduced host abundance. The cheater can grow successfully once mutualist density is lowered and competitive inhibition is reduced.

We see that parameter values can be chosen so that for low nutrient soils, the mutualist always excludes the cheater, but for high nutrient soils the cheater may be able to coexist with or exclude the mutualist. This occurs because at low host densities fungal interactions are relatively more dependent on growth rates (and we have assumed that the mutualists have higher growth rates), while at high host densities fungal interactions are determined more by their competition coefficients. Thus, the advantage in growth rate experienced by the mutualist ensures competitive dominance at low host densities, but not at high host densities. This may explain the decline of beneficial fungi in heavily fertilized systems, such as agricultural fields (Johnson, 1993; Johnson et al., 1997; Helgason et al., 1998).

It should be pointed out that these predictions change if there is a negative correlation between γ and b/d , and thus $b_1/d_1 < b_2/d_2$. This would occur if, for example, the mutualist incurs a net cost when transferring nutrients to its host. In this case, a similar analysis as above would conclude that the cheater excludes the mutualist in the case of low soil fertility, and that increased soil fertility favors the mutualist. The empirical relationship between mycorrhizal growth rates and host benefit is still an open question (Douglas, 1995), so it would be speculative to propose a priori either scenario as more biologically realistic. However, if our model is to agree with the empirically observed shift from mutualism to parasitism across increasing soil fertility, mutualists must have a higher relative growth rate than cheaters.

Table 2
The equilibria (H , P , Q) are listed together with their stability

H	P	Q	Stability
$K = 2$, coexistence, Q cannot invade			
2.3939	6.1817	0	Locally stable
1.333	0	1.6667	Unstable
2.2094	1.1525	2.7125	Locally stable
2.3949	6.1585	0.0159	Unstable
$K = 3$ coexistence			
2.3987	6.1961	0	Unstable
1.6364	0	2.2727	Unstable
2.1995	0.887	2.8556	Locally stable
$K = 20$, Q wins			
2.4503	6.3510	0	Unstable
2.6667	0	4.3333	Locally stable

Parameter values: $\gamma = 5$, $r = 2$, $a_1 = 0.3$, $a_2 = 0.4$, $b_1 = 3$, $b_2 = 2$, $c_1 = 1.650$, $c_2 = 0.6128$, $d_1 = 1$, $d_2 = 1$, $e_1 = 1$, $e_2 = 1$.

4. Discussion

Nonlinear mutualism models that predict a stable equilibrium of host and symbiont have been presented before (Whittaker, 1975; Vandermeer and Boucher, 1978; May, 1981; Soberon and Martinez del Rio, 1981; Wells, 1983). Uniquely, our model is based on a modified predator–prey model, which includes both the cost of exploitation, and the possibility of a benefit conferred to the victim by the exploiter. This allows the model to exhibit both parasitic and mutualistic behavior.

Few models address the factors that control shifts from mutualism to parasitism. Hochberg et al. (2000) present a model that shows striking agreement with our prediction of a shift in the outcome of competition with increased host abundance. Their model of competition between symbionts showed that avirulent (more beneficial) symbionts were favored at low host productivity, and virulent (less beneficial or parasitic) symbionts were favored at high host productivity. This occurs in their model when the avirulent symbiont experiences higher growth (via vertical transmission), while the virulent symbiont is a better competitor (higher horizontal transmission). The similarity between our findings and those of Hochberg et al. (2000) are particularly interesting because Hochberg et al.'s model contains some fundamental differences from our model. For example, in their model symbionts affect growth rates rather than carrying capacity, which is not an explicit parameter, and it is assumed that all hosts are infected with only one symbiont. The agreement of these different models supports the generality of our results. Hernandez (1998) presents a general model, which allows for shifts in interaction types because competition coefficients are allowed to vary (and change sign) as nonlinear functions of population density. The generality of this model precludes further comparison. Zhang (2003) modifies the Lotka–Volterra competition model by introducing density dependent interactions: mutualism at low densities and competition at high densities, which demonstrates that mutualism can facilitate coexistence. This model is intended to apply to interactions between species at the same trophic level, and does not likely apply to interactions between a host and its symbiont, because hosts generally do not have a negative effect on symbionts at high host density. Similarly, Tainaka

et al. (2003) modified the standard Lotka–Volterra model of interspecific competition. Their focus is to investigate the role of a spatial component on stability of equilibria, which precludes further comparisons between our and their approaches. Holland et al. (2002) developed a model using differential equations in which the costs and benefits vary over population densities of interacting symbionts, and applied it to a plant–pollinator mutualism. They note the importance of the type of assumed functional responses for model dynamics. Our model includes a functional response not considered in their paper, namely the effect of one symbiont on the carrying capacity of the other. Empirical characterization of the shape of such functional responses will be an important area of future research.

Fisher and Freedman (1991) consider a mutualism model where the mutualistic interaction is modeled indirectly through “environmental protection,” such that a protector species positively affects the carrying capacity of a protected species once both species exceed a threshold density. Their model, just as ours, includes a mechanism that allows for an increase in carrying capacity of the host species, and shows that this increase in carrying capacity facilitates coexistence between the host and the symbiont. Their paper, however, does not address the shift from mutualism to parasitism observed here nor the interactions between a mutualist and a cheater.

Morris et al. (2003) explored the conditions under which a mutualist and cheater (exploiter) can coexist in a plant–pollinator symbiosis, also using differential equations in which the costs and benefits vary over population densities of interacting symbionts. They found requirements for coexistence similar to those in Lotka–Volterra competition models, such that coexistence is favored when intraspecific competition is greater than interspecific competition. Although their model is for obligate and ours for facultative mutualisms, their conclusions with respect to the role of intra- versus interspecific competition are similar to ours.

Wilson et al. (2003) investigate obligate mutualisms that allows for inclusion of an exploiter, in contrast to the facultative mutualism explored here. Obligate mutualism leads to bistability in the case of a single host and single symbiont; this is not seen in our model where the host always has a positive density in

the absence of the other symbionts. The Wilson et al. model is in discrete time and follows the approach of the Nicholson–Bailey model; the inclusion of an exploiter species leads to complex dynamics that are not exhibited by our model. Their focus is on the role of a spatial component that stabilizes the dynamics, an aspect we did not address.

While much research has addressed the question of how mutualisms may have evolved (Hoeksema and Bruna, 2000), fewer have addressed the related question of how mutualists and cheater can coexist in ecological time (Morris et al., 2003; Wilson et al., 2003). Such coexistence is likely a prerequisite for the evolution of a mutualist in the presence of a cheater, making models, such as ours (for facultative mutualisms) and the ones presented in Morris et al. (2003) and Wilson et al. (2003) (for obligate mutualisms), relevant for exploring factors influencing the evolution of mutualism. For example, our predictions about interspecific competition may be reinterpreted in an evolutionary context to suggest that mutualistic genotypes are relatively favored at low host productivity and cheater genotypes are relatively favored at high host productivity.

Our model has the potential to address other questions. For example, in our analysis, we assumed that the host has no control over how much it should return to the symbiont. Relaxing this assumption could allow the interaction to remain mutualistic even as soil fertility increases.

When applied to plant–mycorrhizae interactions, the model provides two mechanisms for the empirically observed change from a mutualistic to a parasitic interaction as soil fertility increases. First, as benefits to the plant become less important with increasing soil fertility, the interaction between the fungus and its host turns parasitic without changing either the host or the fungus characteristics. Second, competitive interactions between two strains of fungi can show a shift in favor of a cheater as soil fertility increases. This occurs when the mutualist has a higher growth rate, but the cheater is a better competitor. Contrary to the impression commonly given in ecology textbooks (e.g. Stiling, 1999), simple adaptations of the Lotka–Volterra model to mutualism can facilitate coexistence, yield stable equilibria, and offer insight into the ecological dynamics of mutualists.

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Appendix A.

A.1. Analysis of the host–mutualist–cheater system

The model is given by the following set of differential equations

$$\begin{aligned}\frac{dH}{dt} &= rH \left(1 - \frac{H}{K + \gamma P} \right) - a_1 PH - a_2 QH \\ \frac{dP}{dt} &= b_1 HP - d_1 P(1 + e_1 P + c_1 Q) \\ \frac{dQ}{dt} &= b_2 HQ - d_2 Q(1 + e_2 Q + c_2 P)\end{aligned}\quad (\text{A.1})$$

The parameters $r, K, a_1, a_2, b_1, d_1, e_1, b_2, d_2$ and e_2 are positive, and c_1, c_2 and γ are nonnegative. We assume throughout that $K > (d_1/b_1), (d_2/b_2)$. When either P or Q are equal to 0, the system reduces to the two species host–symbiont model. There are thus at least the following three equilibria: the *trivial equilibrium* $(0, 0, 0)$, the equilibrium where the mutualist is absent, $(\bar{H}^Q, 0, \bar{Q})$, and the equilibrium where the cheater is absent, $(\bar{H}^P, \bar{P}, 0)$. We call the latter two equilibria *boundary equilibria*. There might be additional equilibria with $H^* > 0, P^* > 0$, and $Q^* > 0$, called *nontrivial equilibria*.

A.2. Invasibility criteria

To understand the equilibrium behavior, we determine conditions when P (respectively, Q) can invade the boundary equilibrium when Q (respectively, P) is present. If $K > (d_1/b_1)$ and $Q = 0$, then there exists a unique boundary equilibrium $(\bar{H}^P, \bar{P}, 0)$ where $\bar{H}^P > 0$ with $\bar{P} = (1/e_1)((b_1/d_1)\bar{H}^P - 1) > 0$. If we define

$$\begin{aligned}\lambda_1^P &= \frac{1}{e_1} \left(\frac{b_1}{d_1} \bar{H}^P - 1 \right) \quad \text{and} \\ \lambda_2^P &= \frac{1}{e_2} \left(\frac{b_2}{d_2} \bar{H}^P - 1 \right)\end{aligned}$$

then Q can invade the $(\bar{H}^{\bar{P}}, \bar{P}, 0)$ equilibrium if

$$\frac{1}{Q} \frac{dQ}{dt} \Big|_{(\bar{H}^{\bar{P}}, \bar{P}, 0)} = b_2 \bar{H}^{\bar{P}} - d_2(1 + c_2 \bar{P}) > 0$$

This yields the condition

$$c_2 < e_2 \frac{\lambda_2^P}{\lambda_1^P}$$

If $K > (d_2/b_2)$ and $P = 0$, then there exists a unique boundary equilibrium $(\bar{H}^{\bar{Q}}, 0, \bar{Q})$ where $\bar{H}^{\bar{Q}} > 0$ with $\bar{Q} = (1/e_2)((b_2/d_2)\bar{H}^{\bar{Q}} - 1) > 0$. If we define

$$\lambda_1^Q = \frac{1}{e_1} \left(\frac{b_1}{d_1} \bar{H}^{\bar{Q}} - 1 \right) \quad \text{and}$$

$$\lambda_2^Q = \frac{1}{e_2} \left(\frac{b_2}{d_2} \bar{H}^{\bar{Q}} - 1 \right)$$

then a similar invasibility analysis as above shows that P can invade the $(\bar{H}^{\bar{Q}}, 0, \bar{Q})$ equilibrium if and only if

$$c_1 < e_1 \frac{\lambda_1^Q}{\lambda_2^Q}$$

A.3. Dependence of λ_1^P and λ_2^Q on K

The quantities λ_1^P and λ_2^Q are the respective symbiont equilibria of the two-species model. The nontrivial equilibrium (H^*, P^*) of the two-species model is the point of intersection of the host isocline and the symbiont isocline in the positive quadrant of the H - P plane (see panel 1 in Fig. 3). It follows from the algebraic form of the host isocline that as K increases, the host isocline moves to the right (see panel 1 in Fig. 3). Since the symbiont isocline in the H - P plane is a straight line with positive slope, it follows immediately that both H^* and P^* are increasing functions of K . This argument holds for all $\gamma \geq 0$ and thus holds for both the H - P and the H - Q system. This shows that both $\bar{H}^{\bar{P}}$, $\bar{P}$, $\bar{H}^{\bar{Q}}$ and $\bar{Q}$ are increasing functions of K .

A.4. Dependence of $e_2 \lambda_2^P / \lambda_1^P$ and $e_1 \lambda_1^Q / \lambda_2^Q$ on K

Define

$$f_1(x) = e_1 \frac{(b_2/d_2)x - 1}{(b_1/d_1)x - 1} \quad \text{and}$$

$$f_2(x) = e_2 \frac{(b_1/d_1)x - 1}{(b_2/d_2)x - 1}$$

Then $f_1(\bar{H}^{\bar{P}}) = e_2 \lambda_2^P / \lambda_1^P$ and $f_2(\bar{H}^{\bar{Q}}) = e_1 \lambda_1^Q / \lambda_2^Q$. Since we assumed $(b_1/d_1) > (b_2/d_2)$, $f_2(x)$ is a decreasing function for $x > (d_2/b_2)$ and $f_1(x)$ is an increasing function for $x > (d_1/b_1)$. We find that

$$\lim_{x \rightarrow \infty} f_1(x) = e_1 \frac{d_1}{b_1} \frac{b_2}{d_2} \quad \text{and} \quad \lim_{x \rightarrow \infty} f_2(x) = e_2 \frac{d_2}{b_2} \frac{b_1}{d_1}$$

As $K \rightarrow \infty$, $\bar{H}^{\bar{P}} \rightarrow (d_1/b_1)(1 + e_1(r/a_1))$, $\bar{P} \rightarrow (r/a_1)$, $\bar{H}^{\bar{Q}} \rightarrow (d_2/b_2)(1 + e_2(r/a_2))$, and $\bar{Q} \rightarrow (r/a_2)$. Furthermore, we find that

$$\lim_{K \rightarrow \infty} e_2 \frac{\lambda_2^P}{\lambda_1^P} = e_1 \frac{b_2}{d_2} \frac{d_1}{b_1} - \frac{a_1}{r} \left(1 - \frac{b_2}{d_2} \frac{d_1}{b_1} \right) < e_1 \frac{b_2}{d_2} \frac{d_1}{b_1}$$

and

$$\lim_{K \rightarrow \infty} e_1 \frac{\lambda_1^Q}{\lambda_2^Q} = e_2 \frac{b_1}{d_1} \frac{d_2}{b_2} + \frac{a_2}{r} \left(1 - \frac{b_1}{d_1} \frac{d_2}{b_2} \right) > e_2 \frac{b_1}{d_1} \frac{d_2}{b_2}$$

This is summarized in Fig. 5.

A.5. Nontrivial equilibria and stability

The zero isoclines are obtained by setting the time derivatives in Eq. (A.1) equal to 0. We find

$$\frac{dH}{dt} = 0 : \quad H = (K + \gamma P) \left(1 - \frac{a_1}{r} P - \frac{a_2}{r} Q \right)$$

$$\frac{dP}{dt} = 0 : \quad H = \frac{d_1}{b_1} (1 + e_1 P + c_1 Q)$$

$$\frac{dQ}{dt} = 0 : \quad H = \frac{d_2}{b_2} (1 + e_2 Q + c_2 P)$$

The zero isoclines satisfying $(dP/dt) = 0$ and $(dQ/dt) = 0$ are planes in the P - Q - H space. If the two planes intersect, their intersection is a line that can be parameterized by H . We find

$$P = \frac{e_2((b_1/d_1)H - 1) - c_1((b_2/d_2)H - 1)}{e_1 e_2 - c_1 c_2} \quad \text{and}$$

$$Q = \frac{e_1((b_2/d_2)H - 1) - c_2((b_1/d_1)H - 1)}{e_1 e_2 - c_1 c_2}$$

The projection of this line onto the P - Q plane is then given by the equation

$$Q = \frac{(d_1/b_1) - (d_2/b_2)}{e_2(d_2/b_2) - c_1(d_1/b_1)} + \frac{e_1(d_1/b_1) - c_2(d_2/b_2)}{e_2(d_2/b_2) - c_1(d_1/b_1)} P$$

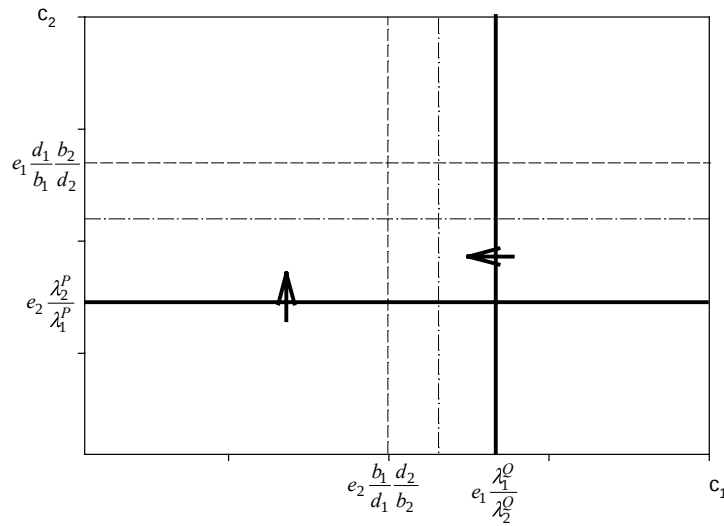


Fig. 5. As K increases, the solid lines move in the direction of the arrows, approaching the broken lines in the limit $K \rightarrow \infty$. The dashed lines are the limits of $f_1(x)$ and $f_2(x)$ as $x \rightarrow \infty$.

Fig. 6 shows the qualitative behavior of the projection of the line of intersection depending on the parameters c_1 and c_2 . We see that the c_1 – c_2 plane is partitioned into four regions, labeled 1–4. Nontrivial equilibria in which the host and both symbiont

densities are positive are the points where the line of intersection of the P and Q isoclines intersects the H isocline in the positive octant. According to Fig. 6, there cannot be such a point of intersection in region 4.

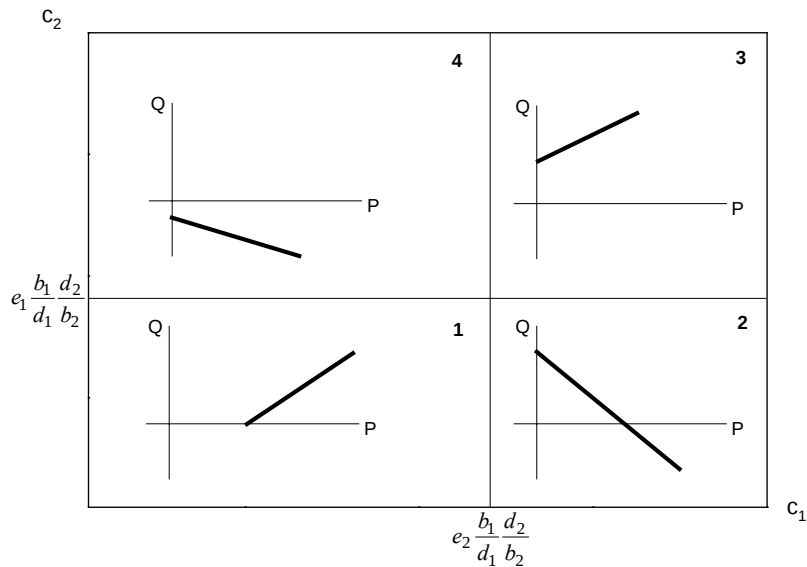


Fig. 6. The coordinate systems within each of the four regions illustrate the qualitative behavior of the line of intersection of the mutualist and cheater isoclines. The horizontal and vertical solid lines are the same as the dashed lines in Fig. 5.

The equation of the projection of the intersection of the Q and H isoclines onto the P – Q plane is given by

$$Q = \frac{K - (d_2/b_2) - ((a_1/r)K + c_2(d_2/b_2) - \gamma)P - \gamma(a_1/r)P^2}{(a_2/r)K + e_2(d_2/b_2) + \gamma(a_2/r)P}$$

The equation of the projection of the intersection of the P and H isoclines onto the P – Q plane is given by

$$Q = \frac{K - (d_1/b_1) - ((a_1/r)K + e_1(d_1/b_1) - \gamma)P - \gamma(a_1/r)P^2}{(a_2/r)K + c_1(d_1/b_1) + \gamma(a_2/r)P}$$

These two intersection curves are qualitatively similar. There is a critical value γ_c so that for $\gamma < \gamma_c$, $(dQ/dP) < 0$ at $P = 0$, and, in fact, $(dQ/dP) < 0$ for all $P \geq 0$, whereas for $\gamma > \gamma_c$, $(dQ/dP) > 0$ at $P = 0$ and Q as a function of P is first increasing, then decreasing for $P > 0$ so that $(dQ/dP) < 0$ when the curve intersects the P -axis (see Fig. 7). Based on the shape of these projection curves, there can thus be no more than one nontrivial equilibrium in region 1 and up to two nontrivial equilibria in regions 2 and 3.

Once an equilibrium is found, its stability can be analyzed using the standard methods (linearization and

eigenvalues). For the general case, this is algebraically quite involved, in particular for the nontrivial equilibria. However, it is possible to predict existence and stability of nontrivial equilibria based on the geometric considerations (described above) and the stability of the boundary equilibria. This can then be checked for specific parameter choices. It allows us to find parameter combinations that have the desired properties, such as the switch from mutualism to parasitism as soil fertility increases. This procedure was used to produce Tables 1 and 2.

For Table 1, we chose the parameter values so that (c_1, c_2) is in region 1 (Fig. 6). For small values of K , the point (c_1, c_2) is above the line $c_1 = e_2\lambda_2^P/\lambda_1^P$ and for large values of K below that line. Table 1 lists some values of K that indicate that the switch from “ P wins” to “coexistence” with unstable boundary equilibria indeed occurs.

For Table 2, we chose parameter values so that (c_1, c_2) is in region 2 (Fig. 6). For small values of K , (c_1, c_2) is above the line $c_2 = e_2\lambda_2^P/\lambda_1^P$ and to the left of the line $c_1 = e_1\lambda_1^Q/\lambda_2^Q$. As K increases, first the line $c_2 = e_2\lambda_2^P/\lambda_1^P$ crosses the point (c_1, c_2) , then the line $c_1 = e_1\lambda_1^Q/\lambda_2^Q$. For the values in Table 2, at small values

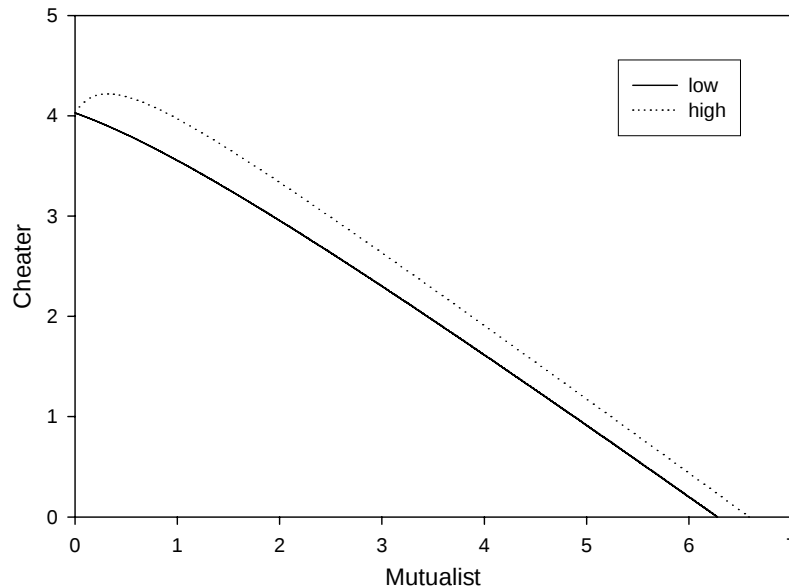


Fig. 7. The qualitative behavior of the line of intersection of the mutualist and the host isoclines depends on γ . The solid line is for γ small, the dashed line for γ large.

of K the cheater cannot invade but since γ is large, there exists a nontrivial, locally stable equilibrium (in addition to a nontrivial, unstable equilibrium). As K increases, both boundary equilibria become unstable and only one nontrivial equilibrium exists. A further increase in K then results in a situation where the cheater can outcompete the mutualist.

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