

## MECHANISMS FOR STABLE COEXISTENCE IN AN INSECT COMMUNITY

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**ABSTRACT.** In this paper, we formulate a three-species ecological community model consisting of two aphid species (*Acyrtosiphon pisum* and *Megoura viciae*) and a specialist parasitoid (*Aphidius ervi*) that attacks only one of the aphids (*A. pisum*). The model incorporates both density-mediated and trait-mediated host-parasitoid interactions. Our analysis shows that the model possesses much richer and more realistic dynamics than earlier models. Our theoretical results reveal a new mechanism for stable coexistence in a three-species community in which any two species alone do not co-exist. More specifically, it is known that, when a predator is introduced into a community of two competing species, if the predator only predaes on the strong competitor, it can allow the weak competitor to survive, but may drive the strong competitor to extinction through over-exploitation. We show that if the weak competitor interferes the predation on the strong competitor through trait-mediated indirect effects, then all three species can stably co-exist.

**1. Introduction.** Ecological communities are influenced by numerous direct and indirect effects among species; these effects collectively determine community composition, structure and functions. Communities of herbivorous insects are complex and their structures are influenced both by the competition for resources and by the action of natural enemies [10], [18], [19]. Parasitoids are amongst the most abundant of all animals; they make up about 1/10 or more of metazoan species and almost no insect species can escape their attack [7]. Parasitoids have been intensively studied because of their importance in the biological control of pests. The relatively simple relationship between attack and recruitment to the next generation makes them valuable model systems in ecology [8].

One way in which parasitoids can influence community structure is when they attack more than one species of host, which then become dynamically linked even if they feed on completely different resources, a phenomenon called apparent competition [9]. Another way is the so-called selective parasitism, in which, parasitoids

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attack only a specific host. For instance, parasitoids only attack the superior competitor of two competing hosts. This relieves the competition pressure experienced by the inferior competitor and may change outcomes of the competition.

Historically, studies on the impacts of food web interactions to community compositions or structure often deal with density-mediated indirect interactions (DMIIs) between predators and their prey. Research on this topic emphasizes the importance of predator regulation of prey density via consumption. Some recent studies have investigated the role played by the trait-mediated indirect interactions (TMIIs) in shaping community structures and compositions [21], [26]. TMIIs is a new way of considering food webs, and may have an equal or greater community-wide effect than DMII [13], [15], [24], [23]. TMIIs are changes in the density of one species that are caused by induced changes in one or more traits of an intervening species [20]. TMIIs occur when one species affects the dynamics of another through causing a change in the behaviors (or other traits) of a third species [27]. Such TMIIs can reinforce or oppose density-mediated effects and have been largely overlooked by community ecologists.

There are many cases where a host is protected from parasitism by a third, non-host species. The best-known example concerns aphids and also other insects that have a mutualistic association with ants: the aphids provide honeydew for the ants and receive protection from at least some natural enemies in return [16]. In this paper, we investigate whether protection from natural enemies can also occur when the third species is a competitor of the host, rather than a mutualist. Such a situation occurs when the competition between two herbivores is asymmetrical, and only the superior competitor is attacked by a parasitoid (this is a relatively common occurrence, as many species of parasitoids have a very narrow host range) [25]. Frank et al [25] discussed a three populations model including two species of aphid (*Acyrtosiphon pisum* and *Megoura viciae*, referred to *A pisum* and *M viciae* for simplicity) competing for the same food plant and a species of a specialist parasitoid (*Aphidius ervi*, referred to *A ervi*) that attacks only one of the aphids (*A pisum*). From laboratory and field experiments, they observed the following

- When the two aphid species compete for resources in the absence of parasitoid, *A pisum* seems to be able to competitively exclude *M viciae*.
- The parasitoid is a solitary species that lays eggs in early-instar aphids. After a period of arrested development, during which the aphid continues to feed and grow, parasitoid larva consume and kill their host, and then spin a cocoon inside the mummified skin of the aphid. A persistent interaction between the host and parasitoid does not seem to be possible.
- When the aphid species and the parasitoid are all present, all three species can coexist.

When three populations are all present, host aphid (*A pisum*) suffers the pressure of interspecific competition in addition to facing the parasitoid's predation. One would expect that it exterminates more quickly than in the absence of its competitor. The field and laboratory observations, however, point to the opposite. To understand possible mechanisms underlying in the third situation, Frank [25] proposed a new

TABLE 1.1. Definition and value of state variable and parameters

Symbol	Definition	Value[25]
$x(t)$	density of the host aphid <i>A pisum</i> at time $t$	
$y(t)$	density of the non-host aphid <i>M viciae</i> at time $t$	
$z(t)$	density of the parasitoid <i>A ervi</i> at time $t$	
$r_1$	the intrinsic growth rate of <i>A pisum</i>	3.22
$r_2$	the intrinsic growth rate of <i>M viciae</i>	2.82
$\alpha_{11}$	the intraspecific competition coefficient of <i>A pisum</i>	$3.84 \times 10^{-4}$
$\alpha_{12}$	the interspecific competition coefficient of <i>M viciae</i>	$3.70 \times 10^{-4}$
$\alpha_{21}$	the interspecific competition coefficient of <i>A pisum</i>	$3.97 \times 10^{-4}$
$\alpha_{22}$	the intraspecific competition coefficient of <i>M viciae</i>	$3.84 \times 10^{-4}$
$d$	natural death rate of the parasitoid <i>A ervi</i>	0.634
$a$	maximum parasitism rate of parasitoid for host	0.281
$s$	conversion rate of host biomass into that of parasitoid	0.5
$\alpha$	encounter rate between parasitoid and host	0.0233
$\beta$	encounter rate between parasitoid and non-hose	0.0434
$\gamma$	encounter rate between parasitoids	1.26

model that combines the Lotka-Volterra competition with predation

$$\begin{aligned}
 \dot{x} &= r_1x(1 - \alpha_{11}x - \alpha_{12}y) - \frac{az}{1 + \alpha x}x, \\
 \dot{y} &= r_2y(1 - \alpha_{21}x - \alpha_{22}y), \\
 \dot{z} &= -dz + \frac{sa z}{1 + \alpha x + \gamma z}x.
 \end{aligned}
 \tag{1.1}$$

The definitions of state variables and parameters in model (1.1) are given in Table 1.1. Model (1.1), however, fails to replicate the observed dynamics. The model predicts that *A pisum* is driven to extinction by its parasitoid and this effect seems to be accelerated by competition with *M viciae* [25]. They [25] argued that there must be mechanisms more complicated than a simple combination of competition and parasitism. Observations of parasitoid behaviors suggested that *A ervi* wastes time when encountering clusters of *M viciae*. Although *A ervi* rarely attempts to attack *M viciae*, when an encounter occurs, the aphid (*M viciae*) displays a vigorous anti-predator response that often results in the parasitoid either being kicked off the plant or abandoning the search for hosts in the area [25]. Selective parasitoid attacks have been suggested to influence the outcome of competition. Earlier experiments have demonstrated that the presence or absence of host-specific parasitoid can determine the outcome of competition at bait stations, and that such interactions may have a major role in structuring ant communities [5]. Werner and Peacor give a series of aquatic examples [22]. After incorporating the effect of *M viciae* into the functional response of the parasitoid, model (1.1) was modified to the following form [25]

$$\begin{aligned}
 \dot{x} &= r_1x(1 - \alpha_{11}x - \alpha_{12}y) - \frac{az}{1 + \alpha x + \beta y}x, \\
 \dot{y} &= r_2y(1 - \alpha_{21}x - \alpha_{22}y), \\
 \dot{z} &= -dz + \frac{sa z}{1 + \alpha x + \beta y + \gamma z}x.
 \end{aligned}
 \tag{1.2}$$

Biological significance of the symbols in model (1.2) are given in Table 1.1. Parameter  $\beta$  can be interpreted as the time wasted when a parasitoid encounters an unsuitable host [25].

Model (1.2) succeeds in predicting coexistence of the three species, which is observed in some cage experiments. This suggests that the stability of the community may be due to a combination of DMII and TMII [25]. There are some shortcomings in model (1.2): the functional response of the parasitoid in (1.2) is independent of  $z$  and model outcomes do not fit the data set quantitatively [25]. The dynamics of model (1.2) have not been studied theoretically.

The principal aim of the present paper is to investigate an improved version of the three-species model (1.2), and systematically explore its rich dynamics. Through both theoretical and numerical analysis, we are able to demonstrate that an combination of DMII and TMII provides a new mechanism for stable coexistence in a three-species community, in which any two species alone can not stably co-exist. More specifically, it is known that, when a predator is introduced into a community of two competing species, if the predator predate on the strong competitor, it will allow the weak competitor to survive, but may drive the strong competitor to extinction through over-exploitation. We show that if the weak competitor interferes the predation on the strong competitor through TMII, then all three species can stably co-exist. This provides a theoretical basis for the field experiments on the community of *A pisum*, *M viciae*, and *A ervi* in [25].

The content of the paper is organized as following. In Section 2, based on (1.2), we develop a more reasonable host-nonhost competitor-parasitoid model and summarize some basic properties of several submodels (competition, predator-prey, etc). Section 3 is devoted to the rich dynamics of the model near the various trivial and semi-trivial equilibria and the theoretical findings are listed as an appendix. Section 4 studies 4 different situations in which the multiple species may or may not coexist and reveal the mechanisms. The paper ends with some discussions and try to place the main findings in the context of some other studies. Throughout this paper, extensive computational results are presented to illustrate or complement our mathematical observations and findings.

**2. The model.** Based on (1.2), we assume that the functional response of the parasitoid is dependent on the density of the parasitoid and the rate at which parasitized host is converted into new parasitoids is directly proportional to the killing rate and yield the following model for the *A pisum*-*M viciae*-*A ervi* community

$$\begin{aligned} \dot{x} &= r_1x(1 - \alpha_{11}x - \alpha_{12}y) - \frac{axz}{1 + \alpha x + \beta y + \gamma z}, \\ \dot{y} &= r_2y(1 - \alpha_{21}x - \alpha_{22}y), \\ \dot{z} &= -dz + \frac{saxz}{1 + \alpha x + \beta y + \gamma z}. \end{aligned} \tag{2.1}$$

Here  $x$  and  $y$  represent two competing hosts or preys (*A pisum* and *M viciae*), and  $z$  a specialist parasitoid or predator (*A ervi*) that attacks only the prey  $x$  (*A pisum*). Such a scenario also includes certain plants and vertebrate herbivores. The functional response of parasitoid,  $ax/(1 + \alpha x + \beta y + \gamma z)$ , is of Beddington-DeAngelis type, and can be derived by the classical Holling time budget arguments or foraging theory [4].

Based on the biological considerations we assume that  $x(0) > 0, y(0) > 0, z(0) > 0$ , and all the parameters in (2.1) are positive. It can be verified that the positive quadrant of  $\mathbb{R}^3$  is invariant with respect to (2.1).

Model (2.1) includes as special cases several different population models. If there is no parasitoid, then (2.1) is the classical two-species Lotka-Volterra competition

system

$$\dot{x} = r_1x(1 - \alpha_{11}x - \alpha_{12}y), \quad \dot{y} = r_2y(1 - \alpha_{21}x - \alpha_{22}y), \quad (2.2)$$

whose dynamics are determined by the intensity of intraspecific competition and interspecific competition of the two hosts, see Table 2.2.

TABLE 2.2. Dynamics of Lotka-Volterra competition system

Cases	Biological significance	Outcomes of competition
(1) $\alpha_{11} > \alpha_{21}$ , $\alpha_{22} < \alpha_{12}$	Intraspecific competition is more intense than interspecific for <i>A pisum</i> , the opposite for <i>M viciae</i>	<i>M viciae</i> precludes <i>A pisum</i> and wins the competition
(2) $\alpha_{11} < \alpha_{21}$ , $\alpha_{22} < \alpha_{12}$	Interspecific competition is more intense than intraspecific for both <i>A pisum</i> and <i>M viciae</i>	either <i>A pisum</i> or <i>M viciae</i> can possibly win the competition depending on initial population sizes
(3) $\alpha_{11} < \alpha_{21}$ , $\alpha_{22} > \alpha_{12}$	Interspecific competition is more intense than intraspecific for <i>A pisum</i> , the opposite for <i>M viciae</i>	<i>A pisum</i> precludes <i>M viciae</i> and wins in competition
(4) $\alpha_{11} > \alpha_{21}$ , $\alpha_{22} > \alpha_{12}$	Intraspecific competition is more intense than interspecific for both <i>A pisum</i> and <i>M viciae</i>	<i>A pisum</i> and <i>M viciae</i> coexist

If there is no non-host aphid, then (2.1) reduces to the predator-prey model with Beddington-DeAngelis type functional response

$$\begin{aligned} \dot{x} &= r_1x(1 - \alpha_{11}x) - \frac{axz}{1 + \alpha x + \gamma z}, \\ \dot{z} &= -dz + \frac{saxz}{1 + \alpha x + \gamma z}, \end{aligned} \quad (2.3)$$

which, together with its generalization, has been extensively studied in the literature [3], [11], [12]. From [11], [12], we know that if

$$d \geq \frac{sa}{\alpha + \alpha_{11}},$$

then the boundary equilibrium  $(1/\alpha_{11}, 0)$  is globally asymptotically stable (GAS). Otherwise, (2.3) has a positive equilibrium which is GAS or has exactly one stable limit cycle when the positive equilibrium is unstable.

The Beddington-DeAngelis functional response in (2.1) includes the Hyperbolic functional response ( $\beta = \gamma = 0$ ), also known as Holling type II, and bilinear functional response ( $\alpha = \beta = \gamma = 0$ ).

**3. Dynamics of model (2.1).** Model (2.1) admits much richer dynamics compared with (2.2) and (2.3) and has several possible equilibria: the extinction equilibrium  $E_0(0, 0, 0)$ , host aphid (*A pisum*) survival equilibrium  $E_x(1/\alpha_{11}, 0, 0)$ , non-host aphid (*M viciae*) survival equilibrium  $E_y(0, 1/\alpha_{22}, 0)$ . More interesting scenarios include the parasitoid disappearance equilibrium  $E_{xy}(x_1^*, y_1^*, 0)$  and the non-host disappearance equilibrium  $E_{xz}(x_2^*, 0, z_2^*)$ . There is also the coexistence of the community equilibrium  $E_{xyz}(x_3^*, y_3^*, z_3^*)$ .

After carrying out standard qualitative analysis of the dynamics of (2.1), we establish sufficient explicit criteria for the existence and locally asymptotic stability of boundary steady states (see Appendix A for details). The expressions of  $E_{xyz}$

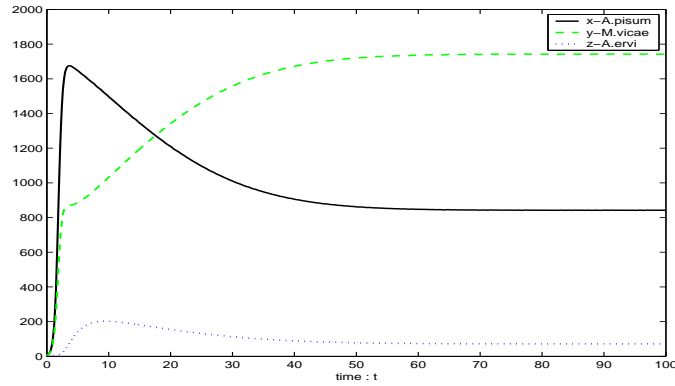
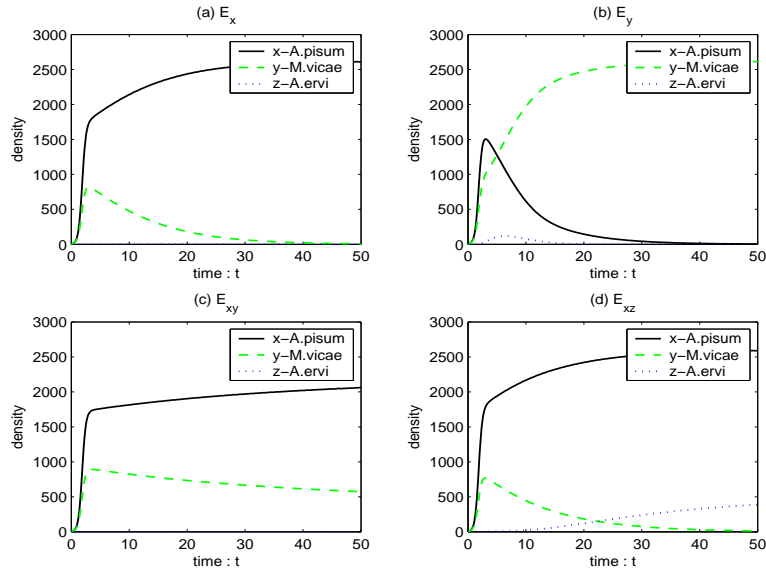
FIGURE 3.1. Stable coexistence of *A pisum*, *M viciae*, and *A ervi*.

FIGURE 3.2. Possible dynamics of (2.1). (a)  $E_x$  is attractor:  $\alpha_{12} = 3.7 \times 10^{-4}$ ;  $\alpha_{21} = 3.8 \times 10^{-4}$ ;  $d = 0.634$ ;  $s = 0.05$ . (b)  $E_y$  is attractor:  $\alpha_{12} = 3.7 \times 10^{-4}$ ;  $\alpha_{21} = 3.97 \times 10^{-4}$ ;  $d = 0.634$ ;  $s = 0.5$ . (c)  $E_{xy}$  is attractor:  $\alpha_{12} = 3.7 \times 10^{-4}$ ;  $\alpha_{21} = 3.97 \times 10^{-4}$ ;  $d = 0.634$ ;  $s = 0.05$ . (d)  $E_{xz}$  is attractor:  $\alpha_{12} = 3.7 \times 10^{-4}$ ;  $\alpha_{21} = 3.97 \times 10^{-4}$ ;  $d = 0.05345$ ;  $s = 0.5$ .

and its stability criteria are too complex to be explicitly expressed in term of the parameters of (2.1). Our mathematical analysis provides some possible candidates for  $E_{xyz}$ . The deterministic nature of the model allows us to carry out systematic numerical studies. Our numerical simulations show that *A pisum*, *M viciae*, and *A ervi* can coexist at the equilibrium  $E_{xyz}$ , see Fig. 3.1. Fig. 3.2 shows other possible dynamics of (2.1). Our simulations are carried out using Matlab. Parameter values used for simulations are given in Table 1.1.

Table 3.3 summarizes and depicts the rich dynamics of (2.1). In view of Table 3.3, the simultaneous extinction of all three populations will never occur since  $E_0$  is

TABLE 3.3. Dynamics of (2.1)

	Existence	Locally asymptotic stability
$E_0$	no condition	unstable (i.e., saddle-node)
$E_x$	no condition	$\alpha_{11} < \alpha_{21}, d > \frac{sa}{\alpha + \alpha_{11}}$
$E_y$	no condition	$\alpha_{22} < \alpha_{12}$
$E_{xy}$	$\delta(\alpha_{11} - \alpha_{21}) > 0,$ $\delta(\alpha_{22} - \alpha_{12}) > 0$	$\delta := a_{11}a_{22} - a_{12}a_{21} > 0,$ $d > \frac{sa(\alpha_{22} - \alpha_{12})}{\alpha(\alpha_{22} - \alpha_{12}) + \beta(\alpha_{11} - \alpha_{21}) + \delta} := d^*$
$E_{xz}$	$d < \frac{sa}{\alpha + \alpha_{11}}$	$s\gamma > \alpha, d > \frac{sa}{\alpha + \alpha_{21}}$

unstable. Such an extinction may occur in nature due to external perturbations that are not considered in the model. If the interspecific competition is stronger than the intraspecific competition ( $\alpha_{21} > \alpha_{11}$ ) for the host *A pisum*, and the parasitoid *A ervi* has high death rate ( $d > sa/(\alpha + \alpha_{11})$ ), then the *A ervi* can not effectively suppress *A pisum*. As a result, *A pisum* preclude its competitor *M viciae*, and tends to its carrying capacity;  $E_x$  is an attractor.

If the interspecific competition is stronger than the intraspecific competition ( $\alpha_{12} > \alpha_{22}$ ) for the non-host *M viciae*, then *M viciae* precludes its competitor *A pisum* even when there is no parasitoid. As a result, *M viciae*'s competition together with *A ervi*'s predation on *A pisum* leads to the extinction of *A pisum*, and then *A ervi* exterminates due to lack of prey/food. Therefore,  $E_y$  is an attractor.

The more interesting scenarios include the host-parasitoid equilibrium  $E_{xz}$  and the hosts-only equilibrium  $E_{xy}$ . If the interspecific competition is stronger than the intraspecific competition for both *A pisum* and *M viciae* ( $\alpha_{11} > \alpha_{21}, \alpha_{22} > \alpha_{12}$ ) and *A ervi* has a relatively high death rate ( $d > d^*$ ), then both the host and the non-host can coexist at  $E_{xy}$  while *A ervi* exterminates due to high death rate.

If the *A pisum*'s interspecific competition is stronger than its intraspecific competition ( $\alpha_{21} > \alpha_{11}$ ) and *A ervi* has moderate death rate, then *A pisum* and *A ervi* can coexist and *M viciae* exterminates due to the strong competition from *A pisum*. That is,  $E_{xz}$  is an attractor.

**4. Coexistence: Density-mediated and trait-mediated indirect effects.** In this section, we discuss mechanisms underlying the extinction and coexistence in the community and impacts of parasitism on interspecific competition, with emphasis on the roles played by density-mediated and trait-mediated indirect effects. In view of the dynamics of the classical Lotka-Volterra two-species competition model (2.2), we will divide our discussion into four cases (c.f. Table 2.2).

**Case 1.** *M viciae* is a dominant superior competitor in interspecific competition when there is no parasitism.

If  $\alpha_{11} > \alpha_{21}, \alpha_{22} < \alpha_{12}$ , i.e., the intraspecific competition is more intense than the interspecific competition for *A pisum* while the opposite for *M viciae*, then *M viciae* wins and *A pisum* exterminates when there is no parasitoids (Table 2.2). If the parasitoid *A ervi* is present, the situation for *A pisum* is worse since *A pisum* suffers not only interspecific competition but also attacks from *A ervi*. As a result, *A pisum* can not survive ( $E_y$  is attractive). In this case, the coexistence of these three species is impossible (Table 3.3).

**Case 2.** Either *A pisum* or *M viciae* can possibly win in interspecific competition depending on their initial population sizes when there is no parasitism.

If  $\alpha_{11} < \alpha_{21}$ ,  $\alpha_{22} < \alpha_{12}$ , i.e., the interspecific competition is more intense than intraspecific for both *A pisum* and *M viciae*, then either *A pisum* or *M viciae* can possibly win in competition depending on initial population sizes (Table 2.2). When there is *A ervi*, which attacks on *A pisum* and weaken the interspecific competition, *A pisum* may possibly lose the dominance in the competition. When *A ervi* has low death rate ( $0 < d < sa/(\alpha + \alpha_{11})$ ), its parasitism can greatly weaken the competition of *A pisum*. As a result, *M viciae* always wins in the competition and precludes *A pisum*. This in turn leads to the extinction of *A ervi* due to a lack of hosts. *M viciae* survives while *A pisum* and *A ervi* exterminates ( $E_y$  is an attractor (Table 2.2). When *A ervi* has a high death rate ( $d > sa/(\alpha + \alpha_{11})$ ), the parasitism of *A ervi* can not effectively weaken the competition of *A pisum*. As a result, both *A pisum* and *M viciae* can win in the interspecific competition depending on initial population levels. Both  $E_x$  and  $E_y$  are local attractors with different attractive regions (Table 3.3).

**Case 3.** *A pisum* is a dominant superior competitor in interspecific competition when there is no parasitism.

Now, we are at the right position to investigate the most interesting case when  $\alpha_{11} < \alpha_{21}$ ,  $\alpha_{22} > \alpha_{12}$ . This indicates that the interspecific competition is more intense than intraspecific competition for *A pisum* while the opposite for *M viciae*. When there is no parasitoid, *A pisum* will always preclude *M viciae* (Table 2.2). In the three-species community, if *A ervi* has high death rate ( $d > sa/(\alpha + \alpha_{11})$ ), it can not effectively suppress *A pisum*. As a result, *A pisum* precludes *M viciae*. *A ervi* exterminates due to high death rate. The three species can not coexist (Fig. 4.1) and  $E_x$  is an attractor (Table 3.3). If *A ervi* has mediate death rate ( $sa/(\alpha + \alpha_{21}) < d < sa/(\alpha + \alpha_{11})$ ), it can not effectively control *A pisum* and *M viciae* is still precluded by *A pisum*. As a result, *A pisum* and *A ervi* can coexist (Fig. 4.1) and  $E_{xz}$  is an attractor (Table 3.3). If *A ervi* has low death rate (i.e.,  $0 < d < sa/(\alpha + \alpha_{21})$ ), *A ervi* can effectively suppress *A pisum* and weaken its interspecific competition, then *A pisum*, *M viciae* and *A ervi* coexist (Fig. 4.1).

In this case, the parasitoid *A ervi* plays a key role in structuring the community and its death rate  $d$  is a key parameter. From the bifurcation curves in Fig. 4.1, one can see that the decrease of death rate can enhance the possibility of coexistence of these three species. That is to say, selective parasitism on dominant competitor enhances the possibility of coexistence. The reason is that the attack on the susceptible host (*A pisum*) from parasitoid (*A ervi*) reduces the growth rate of the superior competitor, and hence reduces the interspecific competition experienced by the non-host (*M viciae*) such that the non-host competitor (*M viciae*) could persist, this is the so-called density-mediated effect. This suggests that a modest decrease in *A pisum* density may be sufficient to promote coexistence.

Can we conclude that the coexistence of *A pisum*, *M viciae* and *A ervi* is solely determined by the density-mediate indirect effect? The answer is no. We proceed with the discussion from a different point of view. We will investigate the impact of the non-host aphid *M viciae*.

Recall that, in (2.1),  $\beta$  reflects the degree of interference which non-host brings to parasitoid. From [11], [12], one knows that *A pisum* and *A ervi* coexist stably in the absence of *M viciae*. In the three-species community, if  $\beta = 0$  in (2.1), i.e., *M viciae* is just a competitor of *A pisum* and has no effects on *A ervi*, then *A pisum*, *M viciae* and *A ervi* coexist but the population sizes of *A pisum* and *A ervi* are very small (see Fig. 4.2). *A pisum* is driven to very low density by parasitism, which



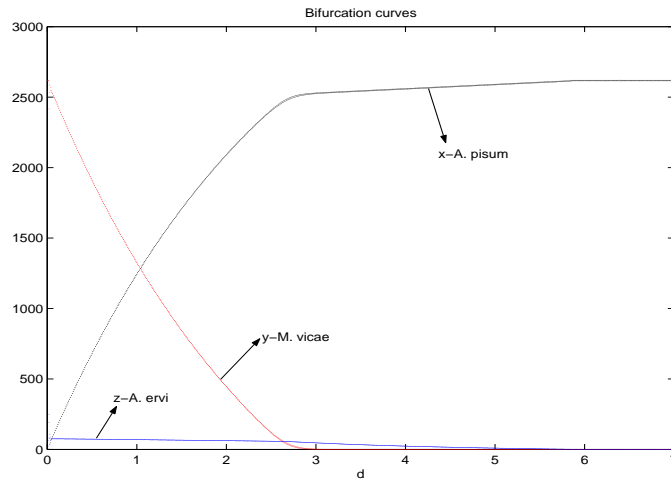


FIGURE 4.1. Bifurcation curves against  $d$  (dynamics of saturated population level changing with different  $d$ ), which represents the impact of  $A\ ervi$  on the community when  $A\ pisum$  precludes  $M\ viciae$  in the absence of  $A\ ervi$ : DMII. The values of other parameters are defined in Table 1.1.

seems to be accelerated by competition with  $M\ viciae$ . However, these findings are not consistent with the cage experiments in [25]. There must be relationships in addition to DMII occurring in the three-species community.  $A\ pisum$  and  $M\ viciae$  are frequently found feeding on the same host plant. Observations of parasitoid behaviors suggested that  $M\ viciae$  interferes the parasitism of  $A\ ervi$  although  $A\ ervi$  rarely attempts to attack  $M\ viciae$ . When an encounter occurs,  $M\ viciae$  displays a vigorous anti-predator response that often results in the parasitoid either being kicked off the plant or abandoning the search for  $A\ pisum$  in the area [25].

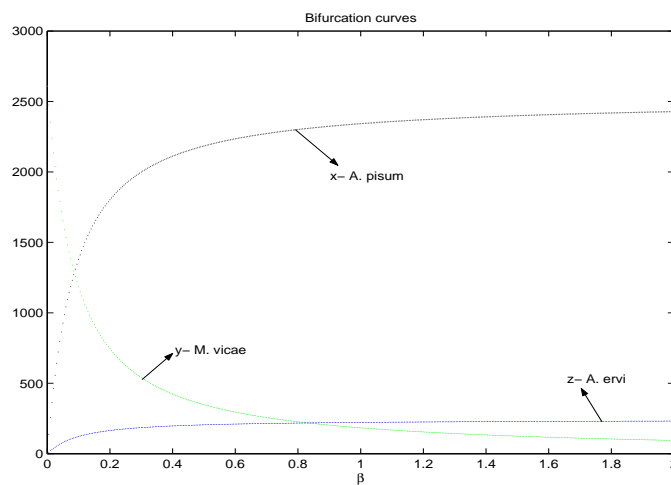


FIGURE 4.2. Bifurcation curves against  $\beta$  (dynamics of saturated population level changing with different  $\beta$ ), which indicates the impact of  $\beta$  on the coexistence: TMII. The values of other parameters are defined in Table 1.1.

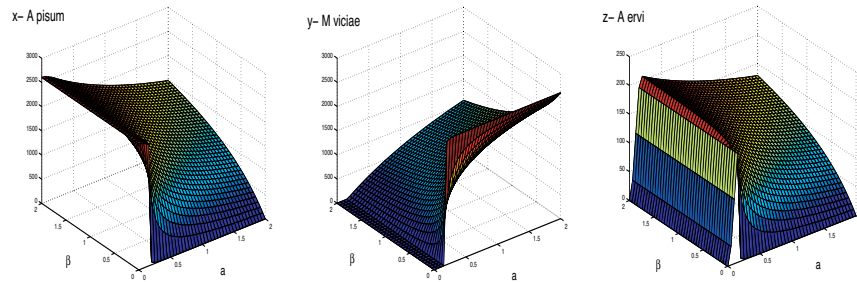


FIGURE 4.3. Bifurcation surfaces against  $a$  and  $\beta$  (dynamics of saturated population level changing with different  $a$  and  $\beta$ ), which represent the impact of *A ervi* on the community when *A pisum* precludes *M viciae* in the absence of *A ervi*. The values of other parameters are defined in Table 1.1 except the bifurcation parameters.

When  $\beta > 0$ , the three populations stably coexist at relatively high population levels (Fig. 4.2). For example, when  $\beta = 0.5$  (Fig. 4.2), the effective interference of *M viciae* with *A ervi* reduces the searching efficiency of *A ervi*, weakens the parasitism of *A ervi* on *A pisum* and prevents *A ervi* from over-exploiting *A pisum*, and hence *A pisum* increases quickly. Then *A pisum* asserts severe competition on *M viciae* and leads to the decrease of *M viciae* and hence weakens the interference of *M viciae* with *A ervi*. When *M viciae* is sufficiently suppressed by the superior competition *A pisum*, *A ervi* is released from the interference of *M viciae* and increases. As a result, the three populations coexist at the positive equilibrium  $E_{xyz}$ .

From Fig. 4.3 (e.g.,  $\beta = 0.5$ ), one can see that *A ervi* can over-parasitize *A pisum* at very low parasitism rate when *M viciae* has no interference with *A ervi*, while, when *M viciae* interferes with *A ervi*, it is not easy for *A ervi* to over-parasitize its host since *M viciae*'s interference with *A ervi* can effectively prevent *A ervi* from over-parasitizing its host *A pisum*. The bifurcation curves or surfaces (Fig. 4.2 and Fig. 4.3) show that DMIs alone is not sufficient to produce the coexistence of *A pisum*, *M viciae* and *A ervi* and the stable coexistence of the full community is due to a combination of density-mediated indirect effect: attacks on *A pisum* from *A ervi* reduces the interspecific competition experienced by *M viciae*, and trait-mediated indirect effect: the presence of *M viciae* alters the environmental conditions and its interference with *A ervi* reduces the searching efficiency of *A ervi* and prevents *A ervi* from over-parasitizing its host.

From Fig. 4.3, we find that, when *A ervi* has low maximum parasitism rate ( $0 < a < d(\alpha + \alpha_{11})/s$ ), *A ervi* can not effectively parasitize *A pisum*, and hence eventually exterminates and *A pisum* precludes *M viciae*. When *A ervi* has a mediate maximum parasitism rate ( $d(\alpha + \alpha_{11})/s < a < d(\alpha + \alpha_{21})/s$ ), *A ervi* can successfully parasitize *A pisum*, but can not effectively suppress *A pisum*. As a result, *A pisum* can still precludes *M viciae*. When *A ervi* has a high maximum parasitism rate ( $a > d(\alpha + \alpha_{21})/s$ ), it can successfully parasitize *A pisum* and effectively suppress *A pisum*. Then the species can coexist at some positive equilibrium. A necessary condition for the coexistence of these species is  $a > d(\alpha + \alpha_{21})/s$  (see Table 3.3). When  $a > d(\alpha + \alpha_{21})/s$ , the interference of *M viciae* with *A ervi* is

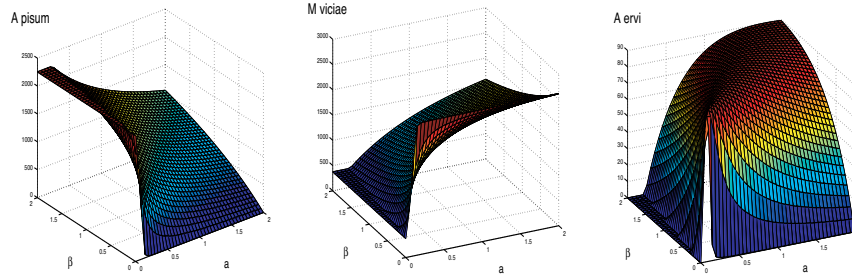


FIGURE 4.4. Bifurcation surfaces against  $a$  and  $\beta$  (dynamics of saturated population level changing with different  $a$  and  $\beta$ ), which indicate the impact of  $A\ ervi$  on the community when  $A\ pisum$  and  $M\ viciae$  coexist in the absence of  $A\ ervi$ . Here  $\alpha_{11} = \alpha_{22} = 3.82 \times 10^{-4}$ ,  $\alpha_{12} = 3.7 \times 10^{-4}$ ,  $\alpha_{21} = 3.8 \times 10^{-4}$ ,  $s = 0.05$  and the values of other parameters are defined in Table 1.1

positive to the coexistence of the community (see Fig. 4.3) and enhances the coexistence. Fig. 4.3 show that the increase of maximum parasitism rate of  $A\ ervi$  is positive to  $M\ viciae$  since the parasitism of  $A\ ervi$  weakens the competition of  $A\ pisum$ . The increase of maximum parasitism rate of  $A\ ervi$  is negative to  $A\ pisum$  and hence is also negative to itself due to lacking host to parasitize. The increase of interference of  $M\ viciae$  with  $A\ ervi$  is negative to  $A\ ervi$  by reducing its search efficiency, which leads to somewhat release of  $A\ pisum$  from  $A\ ervi$ 's predation. Whence  $A\ pisum$  competes with  $M\ viciae$  more intensively. It is interesting to note that the interference of  $M\ viciae$  with  $A\ ervi$  is positive to  $A\ pisum$  although  $M\ viciae$  competes with  $A\ pisum$  for some common resources.

**Case 4.** Both  $A\ pisum$  and  $M\ viciae$  coexist in interspecific competition when there is no parasitism.

If  $\alpha_{11} > \alpha_{21}$ ,  $\alpha_{22} > \alpha_{12}$ , i.e., the intraspecific competition is more intense than the interspecific competition for both  $A\ pisum$  and  $M\ viciae$ , then  $A\ pisum$  and  $M\ viciae$  coexist (Table 2.2). Now assume that  $A\ ervi$  is in the community. When  $A\ ervi$  has a high death rate ( $d > d^*$ ), it can not assert effective attacks on  $A\ pisum$  and can not survive. So,  $A\ pisum$  and  $M\ viciae$  coexist at  $E_{xy}$ ;  $E_{xy}$  is an attractor (Table 3.3). When  $A\ ervi$  has a low death rate, it can effectively invade  $A\ pisum$  and then the three species can stably coexist (Fig. 4.4).

From Fig. 4.4 with  $\beta = 0$ , we find that if  $M\ viciae$  has no interference effect on  $A\ ervi$  ( $\beta = 0$ ), then, when  $A\ ervi$  has high maximum parasitism rate,  $A\ ervi$  can over-parasitize  $A\ pisum$  and drive  $A\ pisum$  to very low level (almost extinction). In this case, sufficient parasitism weakens the intensity of competition of  $A\ pisum$  and leads to a quick increase of  $M\ viciae$ , but it can not turn  $M\ viciae$  from an inferior competitor to a superior competitor to precludes  $A\ pisum$ , although  $A\ pisum$  and  $A\ ervi$ ' population levels are very low (one should note that the saturated population size is not zero). From Fig. 4.4 (e.g.,  $\beta = 0.5$  and  $\beta = 1$ ), we find that, when  $M\ viciae$  interferes with  $A\ ervi$  and assert negative impact on  $A\ ervi$ 's searching efficiency ( $\beta > 0$ ), in order to parasitize successfully and to coexist with  $A\ pisum$  and  $M\ viciae$ ,  $A\ ervi$  must have sufficiently high maximum parasitism rate, i.e.,  $a > d[\alpha(\alpha_{22} - \alpha_{12}) + \beta(\alpha_{11} - \alpha_{21}) + \delta] / [s(\alpha_{22} - \alpha_{12})]$ , which depends on  $\beta$  (see  $E_{xy}$  in Table 3.3). Otherwise,  $A\ ervi$  can not successfully parasitize and  $A\ pisum$  and  $M\ viciae$  coexist ( $E_{xy}$  is attractive, see Table 3.3). In this case, when other parameters

are fixed, the relationship between  $a$  and  $\beta$  determines whether these three species can coexist. When *A ervi* has a small maximum parasitism rate  $a$ , for example,  $a$  is greater than but close to  $d[\alpha(\alpha_{22} - \alpha_{12}) + \delta]/[s(\alpha_{22} - \alpha_{12})]$ , the interference of *A ervi* is negative to the coexistence of three species (see Fig. 4.4 with  $a$  being a little bit smaller than 0.2) while, when *A ervi* has a high maximum parasitism rate  $a$ , the interference of *A ervi* is positive to the coexistence (see Fig. 4.4).

From the bifurcation surfaces in Fig. 4.4, we find that the maximum parasitism rate  $a$  of *A ervi* and the interference  $\beta$  of *M viciae* with *A ervi*, have the same effects on the dynamics of as those in Case 3, namely, greater  $a$  is negative to *A pisum* and *A ervi* and is positive to *M viciae*, while greater  $\beta$  is negative to *M viciae* and is positive to *A pisum* and *A ervi*.

The preceding analysis indicates that the impact of parasitism on interspecific competition is very complicated and both density-mediated and trait-mediated indirect interactions between species play an important role in structuring ecological communities.

## 5. Discussions.

**5.1. Main findings.** In this paper, based on existing models, we have developed a plausible model (2.1) to describe the dynamics of a three-species host-nonhost-parasitoid community, in which only the superior competitor is attacked by a natural enemy, and to understand possible mechanisms underlying extinction and coexistence of the community. Our model overcomes several model formulation problems in earlier models. We show that (2.1) admits richer and more realistic dynamics. Although our model is a simplified representation of real ecological communities, neglecting, for example, spatial processes, age-structure effects, and competition from additional host and parasitoid species, we believe that it provides a useful first step in explaining the observed dynamics in laboratory and field experiments.

Our theoretical analysis of model (2.1) shows that a combination of density-mediated and trait-mediated indirect effects contributes to the stability of the community although any two of three species are unable to persist. In the three-species community considered in our model, there are two competing species in which the superior competitor will drive the inferior competitor to extinction. When a natural predator of the superior competitor is introduced, the predation reduces the growth rate of the superior competitor and hence reduces the interspecific competition for the inferior competitor so that the inferior competitor could survive and all three species can co-exist (DMIIs). This is commonly known as predator mediated co-existence [2], [17]. However, predation and competition will normally drive the density of both competitors to very low levels, as shown in Figure 4.2 for  $\beta$  small. Our new finding is the following: if the presence and behaviors of the inferior competitor interfere the predation on the superior competitor (TMIIIs), then all three species can stably co-exist at relatively high population densities, as shown in Figure 4.2 for  $\beta$  large. Our finding provides a theoretical basis for the cage experiments in [25]. The preferential parasitism on the superior *A pisum* allows the inferior *M viciae* to escape from competitive exclusion, while *M viciae*'s behaviors interfere the the predation of *A ervi* on *A pisum* and prevent overexploiting of *A pisum*.

**5.2. Impacts of predation on interspecific competition.** As we mentioned previously, although we focus on an insect community and refer  $x, y$  and  $z$  to *A pisum*, *M viciae* and *A ervi*, respectively, our model (2.1) can be used to model the

predator-prey interactions with two competitive preys and one specialist predator attacking only one of the preys. We call them prey, competitor and predator, respectively.

Competition and predation are two basic and important interspecific interactions in real ecosystems. Predation is one of the factors believed to have a major impact on competitive interactions. What will happen when both competition and predation act simultaneously, as is typical in natural ecosystems? Ecologists working with a range of organisms and environments have carried out many controlled field experiments. These studies show that the effects of competition in the presence of predators are less than those in the absence of predators [6]. Much remains to be learned about the interaction between predation and interspecific competition, both theoretically and empirically [1]. In order to understand the interaction between predation and competition, greater attention should be paid to determining the impacts of predation on interspecific competition and to distinguish different mechanisms by which predation alters interspecific competition among prey species [1].

From our studies in Section 4, we arrive at the following conclusions. If  $\alpha_{11} > \alpha_{21}$ ,  $\alpha_{22} < \alpha_{12}$  or if  $\alpha_{11} < \alpha_{21}$ ,  $\alpha_{22} < \alpha_{12}$ , the predators increase the strength of interspecific competition or promote the competition exclusion, the prey is excluded by its competitor. Particularly, if  $\alpha_{11} < \alpha_{21}$ ,  $\alpha_{22} < \alpha_{12}$ , then either prey or its competitor can win the competition when there is no predator. However, when the predators are presented, the prey is precluded by its competitor.

If  $\alpha_{11} < \alpha_{21}$ ,  $\alpha_{22} > \alpha_{12}$ , the prey will be precluded by its competitor even when there is no predation on the prey. When the predator appears in the community, high enough predation can effectively suppress the prey and weaken its interspecific competitive strength and hence enhance the possibility of the stable coexistence of the whole community. In this case, the predator has positive effect on the stable coexistence of the community. However, the predator can overexploit its prey and coexist with the prey at some very low population level if the competitor has no effects on the predator. The interference of the competitor can effectively prevent the predator from overexploiting its prey and increase the population level at coexistence.

If  $\alpha_{11} > \alpha_{21}$ ,  $\alpha_{22} > \alpha_{12}$ , then the prey and its competitor coexist in the absence of the predator. In the three species community, TMIs between the competitor and the predator can effectively prevent the predator from overexploiting its prey.

To conclude, our theoretical and numerical studies show that the predators (parasitoid) may promote or hinder the interspecific competition, and the probability of coexistence of the community depends on the mechanism and the details of the process of predation (parasitism) and interspecific competition. Selective predation (parasitism) on superior competitors can increase the chance for stable coexistence of the community due to a combination of density-mediated and trait-mediated indirect interactions.

**5.3. Implications for biological invasion.** There are interesting problems concerning the possibility of invasion of alien species, and the control or eradication of the invading alien species in order to protect native species. In the setting of biological invasion, variables  $x$ ,  $y$  and  $z$  can represent native prey, alien competitor, and native predator, respectively.

We discuss possible mechanisms for alien competitor's invasion. When the alien competitor is a superior competitor, it can successfully invade into the community and preclude the native prey and leads to the extinction of the native predator.

When the native prey is the superior competitor or the native prey and the alien competitor coexist in the absence of the native predator, the situation is more interesting. If the alien competitor has no effect on the native predator, then the native predator can overexploited the native prey and allow the alien competitor to successfully invade. If the alien competitor has strong interference with the native predator, and can effectively reduce the native predator's searching efficiency and prevent the native predator from overexploited the native prey, then the alien competitor can also invade and coexist with the native prey and the native predator as a community. However, the alien competitor's interference with the native predator reduces the chance of its invasion.

From the bifurcation surface for the alien competitor *M. viciae* in Fig. 4.3 and 4.4, we find that the predation of the native predator can help the alien competitor with invasion (increase of  $a$  is positive to the alien competitor) while the alien competitor's interference with the native predator prevents itself from invasion (the increase of  $\beta$  is negative to the alien competitor). When the native prey is superior competitor, if the predation rate  $a$  is somewhat small, the native predator can not effectively suppress the native prey and the native prey preclude the alien competitor and prevent the invasion of the alien competitor. To conclude, the existence of native predator is positive to the alien competitor's invasion while the native prey's competition and the alien competitor's interference with the native predator are negative to the alien competitor's invasion.

Although much progress has been seen in the study of biological invasion, ecologists still pursue fundamental questions such as why some particular alien species become widespread and abundant [14]. Several mechanisms are proposed to explain the invasion of alien species. The most straightforward and intuitively appealing explanation for the rapid establishment and proliferation of alien species is that they are released from the effects of their natural enemies. This is the so-called enemy release hypothesis. In the ecological community modeled by (2.1), the alien competitor has no natural enemy in the community. However, the invasion of the alien competitor is due to the weakness of native competitors instead of the lack of natural enemies. Our proceeding discussions argue against a simple relationship between the enemy release and the invasion or the abundance alien species.

Next, we assume that an alien competitor has successfully invaded and coexists with the native competitor. We focus on the case that the native prey is a superior competitor or the native prey and the alien competitor can coexist in the absence of the native predator since the other two cases are very trivial.

The harm caused by alien invasive species is widely known, and control programs are largely recognized as the best way to restore ecosystems [14]. When possible, eradication is the favored approach. However, the ecological context of eradication is very complex and there is also evidence that, without sufficient planning, successful eradications can have many undesired and unexpected impacts [28]. Our studies here show such a case. The control or removal of an alien competitor can possibly release the native predator from the interference caused by the alien competitor through the TMIs, leads to overexploitation of the native prey and destabilizes the whole community.

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**Appendix A. Existence and local asymptotic stability of equilibria.** Model (2.1) has several possible equilibria: the extinction equilibrium  $E_0(0, 0, 0)$ , host (*A pisum*) survival equilibrium  $E_x(1/\alpha_{11}, 0, 0)$ , non-host (*M viciae*) survival equilibrium  $E_y(0, 1/\alpha_{22}, 0)$ . More interesting scenarios include the parasitoid disappearance equilibrium  $E_{xy}(x_1^*, y_1^*, 0)$ , where  $x_1^*, y_1^*$  satisfy

$$1 - \alpha_{11}x - \alpha_{12}y = 0, \quad 1 - \alpha_{21}x - \alpha_{22}y = 0, \quad (\text{A.1})$$

and the non-host disappearance equilibrium  $E_{xz}(x_2^*, 0, z_2^*)$ , where  $x_2^*, z_2^*$  satisfy

$$r_1(1 - \alpha_{11}x) - \frac{az}{1 + \alpha x + \gamma z} = 0, \quad -d + \frac{sax}{1 + \alpha x + \gamma z} = 0. \quad (\text{A.2})$$

There is also the coexistence of the community equilibrium  $E_{xyz}(x_3^*, y_3^*, z_3^*)$ , where  $x_3^*, y_3^*, z_3^*$  satisfy

$$\begin{aligned} r_1(1 - \alpha_{11}x - \alpha_{12}y) &= \frac{az}{1 + \alpha x + \beta y + \gamma z}, \\ r_2(1 - \alpha_{21}x - \alpha_{22}y) &= 0, \\ -d + \frac{sax}{1 + \alpha x + \beta y + \gamma z} &= 0. \end{aligned} \quad (\text{A.3})$$

The local stability of these equilibria is determined by the spectrum of the Jacobian matrix of (2.1),

$$J(x, y, z) = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix},$$

where

$$\begin{aligned} a_{11} &= r_1(1 - 2\alpha_{11}x - \alpha_{12}y) - \frac{az(1 + \beta y + \gamma z)}{(1 + \alpha x + \beta y + \gamma z)^2}, \\ a_{12} &= -r_1\alpha_{12}x + \frac{\beta axz}{(1 + \alpha x + \beta y + \gamma z)^2}, \quad a_{13} = -\frac{ax(1 + \alpha x + \beta y)}{(1 + \alpha x + \beta y + \gamma z)^2}, \\ a_{21} &= -r_2\alpha_{21}y, \quad a_{22} = r_2(1 - \alpha_{21}x - 2\alpha_{22}y), \quad a_{23} = 0, \\ a_{31} &= \frac{saz(1 + \beta y + \gamma z)}{(1 + \alpha x + \beta y + \gamma z)^2}, \quad a_{32} = -\frac{s\beta axz}{(1 + \alpha x + \beta y + \gamma z)^2}, \\ a_{33} &= -d + \frac{sax(1 + \alpha x + \beta y)}{(1 + \alpha x + \beta y + \gamma z)^2}. \end{aligned}$$



In particular

$$J(E_0) = J(0, 0, 0) = \begin{pmatrix} r_1 & 0 & 0 \\ 0 & r_2 & 0 \\ 0 & 0 & -d \end{pmatrix},$$

which leads to the claim that  $E_0$  is always an unstable saddle node.

At  $E_x$  and  $E_y$  we have

$$J(E_x) = \begin{pmatrix} -r_1 & -r_1 \frac{\alpha_{12}}{\alpha_{11}} & -\frac{a}{\alpha_{11} + \alpha} \\ 0 & r_2(1 - \frac{\alpha_{21}}{\alpha_{11}}) & 0 \\ 0 & 0 & -d + \frac{sa}{\alpha_{11} + \alpha} \end{pmatrix}$$

and

$$J(E_y) = \begin{pmatrix} r_1(1 - \frac{\alpha_{12}}{\alpha_{22}}) & 0 & 0 \\ -r_2 \frac{\alpha_{21}}{\alpha_{22}} & -r_2 & 0 \\ 0 & 0 & -d \end{pmatrix},$$

respectively, we thus arrive at the following results.

**Proposition 1.**  $E_x(1/\alpha_{11}, 0, 0)$  and  $E_y(0, 1/\alpha_{22}, 0)$  always exist. If

$$\alpha_{21} > \alpha_{11}, \quad d > \frac{sa}{\alpha + \alpha_{11}},$$

then  $E_x$  is locally asymptotically stable (LAS). If  $\alpha_{12} > \alpha_{22}$ , then  $E_y$  is LAS.

**Proposition 2.** Let  $\delta := a_{11}a_{22} - a_{12}a_{21}$ . If

$$\delta(\alpha_{22} - \alpha_{12}) > 0, \quad \delta(\alpha_{11} - \alpha_{21}) > 0,$$

then  $E_{xy}$  exists. Moreover, if

$$\delta > 0, \quad d > \frac{sa(\alpha_{22} - \alpha_{12})}{\delta + \alpha(\alpha_{22} - \alpha_{12}) + \beta(\alpha_{11} - \alpha_{21})},$$

then  $E_{xy}$  is LAS.

*Proof.* Solving (A.1) produces

$$x_1^* = \frac{\alpha_{22} - \alpha_{12}}{\delta} > 0, \quad y_1^* = \frac{\alpha_{11} - \alpha_{21}}{\delta} > 0.$$

With the help of (A.1), one can rewrite  $J(E_{xy})$  to

$$J(E_{xy}) = \begin{pmatrix} -r_1\alpha_{11}x_1^* & -r_1\alpha_{12}x_1^* & -\frac{\alpha x_1^*}{1 + \alpha x_1^* + \beta y_1^*} \\ -r_2\alpha_{21}y_1^* & -r_2\alpha_{22}y_1^* & 0 \\ 0 & 0 & -d + \frac{sax_1^*}{1 + \alpha x_1^* + \beta y_1^*} \end{pmatrix}.$$

Therefore, the assumptions of the theorem imply

$$a_{33} < 0, \quad a_{11} + a_{22} < 0, \quad a_{11}a_{22} - a_{12}a_{21} = \delta > 0,$$

and thus all three characteristic roots of  $J(E_{xy})$  have negative real parts. Therefore,  $J(E_{xy})$  is LAS.  $\square$

**Theorem A.1.** *Assume that*

$$0 < d < \frac{sa}{\alpha + \alpha_{11}},$$

*then  $E_{xz}$  exists. Moreover, if*

$$s\gamma > \alpha, \quad d > \frac{sa}{\alpha + \alpha_{21}},$$

*then  $E_{xz}$  is local asymptotically stable.*

*Proof.* First, we prove the existence of  $E_{xz}$ . Note that  $x_2^*$  and  $z_2^*$  satisfy (A.2), and  $(x_2^*, z_2^*)$  is the intersection of the following two curves

$$l_1 : z = \frac{(sa - d\alpha)}{d\gamma}x - \frac{1}{\gamma}, \quad l_2 : z = \frac{r_1s}{d}x(1 - \alpha_{11}x).$$

Consider the function defined by

$$F(x) = \frac{r_1s}{d}x(1 - \alpha_{11}x) - \frac{(sa - d\alpha)}{d\gamma}x + \frac{1}{\gamma}.$$

We have

$$F\left(\frac{d}{sa - d\alpha}\right) > 0, \quad F\left(\frac{1}{\alpha_{11}}\right) < 0.$$

By the Intermediate Value Theorem, there exists

$$x_2^* \in \left(\frac{d}{sa - d\alpha}, \frac{1}{\alpha_{11}}\right)$$

such that  $F(x_2^*) = 0$ . The uniqueness of  $x_2^*$  is obvious. In addition, it is clear that

$$z_2^* = \frac{r_1s}{d}x(1 - \alpha_{11}x_2^*) > 0.$$

The proof of the existence of  $E_{xz}$  is complete.

The Jacobian of (2.1) at  $E_{xz}$  is

$$J(E_{yz}) = J(x^*, 0, z^*) = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ 0 & a_{22} & 0 \\ a_{31} & a_{32} & a_{33} \end{pmatrix}$$

where

$$\begin{aligned} a_{11} &= -r_1\alpha_{11}x^* + \frac{a\alpha x^* z^*}{(1 + \alpha x^* + \gamma z^*)^2}, \quad a_{12} = -r_1\alpha_{12}x^* + \frac{a\beta x^* z^*}{(1 + \alpha x^* + \gamma z^*)^2}, \\ a_{13} &= -\frac{ax^*(1 + \alpha x^*)}{(1 + \alpha x^* + \gamma z^*)^2}, \quad a_{22} = r_2(1 - \alpha_{21}x^*), \quad a_{31} = \frac{sa z^*(1 + \gamma z^*)}{(1 + \alpha x^* + \gamma z^*)^2}, \\ a_{32} &= -\frac{sa\beta x^* z^*}{(1 + \alpha x^* + \gamma z^*)^2}, \quad a_{33} = -\frac{sa\gamma x^* z^*}{(1 + \alpha x^* + \gamma z^*)^2}. \end{aligned}$$

If  $s\gamma > \alpha$ , we can show that

$$\begin{aligned} a_{11} + a_{33} &= -r_1\alpha_{11}x^* - \frac{(sa\gamma - a\alpha)x^* z^*}{(1 + \alpha x^* + \gamma z^*)^2} < 0, \\ a_{11}a_{33} - a_{13}a_{31} &= \frac{r_1\alpha_{11}sa\gamma(x^*)^2 z^*}{(1 + \alpha x^* + \gamma z^*)^2} + \frac{sa^2 x^* z^*}{(1 + \alpha x^* + \gamma z^*)^3} > 0. \end{aligned}$$

In addition,

$$a_{22} = r_2(1 - \alpha_{21}x^*) < r_2\left(1 - \frac{d\alpha_{21}}{sa - d\alpha}\right) = r_2\frac{sa - (\alpha + \alpha_{21})d}{sa - d\alpha} < 0.$$

Therefore,  $E_{xz}$  is locally asymptotically stable.  $\square$

Next, we turn to the positive equilibrium  $E_{xyz} = (x_3^*, y_3^*, z_3^*)$ . From (A.3), we know that  $(x_3^*, z_3^*)$  is the intersection of the following curves

$$l_3 : z = \frac{r_1 s}{d} x \left[ 1 - \frac{\alpha_{12}}{\alpha_{22}} + \frac{\alpha_{12}\alpha_{21} - \alpha_{11}\alpha_{22}}{\alpha_{22}} x \right] = \frac{r_1 s}{d\alpha_{22}} x(\alpha_{22} - \alpha_{12} - \delta x),$$

$$l_4 : z = \frac{1}{d\gamma} \left( sa - d\alpha + \frac{d\beta\alpha_{21}}{\alpha_{22}} \right) x - \frac{1}{\gamma} \left( 1 + \frac{\beta}{\alpha_{22}} \right)$$

in the first quadrant of  $xz$  plane. Here

$$y_3^* = \frac{1 - \alpha_{21}x_3^*}{\alpha_{22}}$$

must be positive, so  $x_3^*$  must satisfy

$$x_3^* < \frac{1}{\alpha_{21}}.$$

It can be verified that  $l_3$  and  $l_4$  always have two intersections in the  $xz$  plane if  $\delta > 0$ . Using a similar arguments as in the proof of Theorem A.1, we can establish the following result, which gives the existence of intersections of  $l_3$  and  $l_4$  in the first quadrant of the  $xz$  plane.

**Theorem A.2.**

- If  $\delta > 0$ ,  $\alpha_{22} > \alpha_{12}$ ,  $0 < x_1 < x_2$ , then  $l_3$  and  $l_4$  have a unique intersection in the first quadrant of the  $xz$  plane with  $x_1 < x_3^* < x_2$  (Fig. A.5(a)).
- If  $\delta < 0$ ,  $\alpha_{22} < \alpha_{12}$ ,  $0 < x_1 < x_2$ , then  $l_3$  and  $l_4$  have a unique intersection in the first quadrant of the  $xz$  plane with  $x_3^* > x_2$  (Fig. A.5(b)).
- If  $\delta < 0$ ,  $\alpha_{22} > \alpha_{12}$ ,  $\Delta > 0$ , then  $l_3$  and  $l_4$  have two intersections in the first quadrant of the  $xz$  plane (Fig. A.5(c)).
- If  $\delta < 0$ ,  $\alpha_{22} > \alpha_{12}$ ,  $\Delta = 0$ , then  $l_3$  and  $l_4$  have a unique intersection in the first quadrant of the  $xz$  plane.
- If one of the following conditions is satisfied,
  - $\delta > 0$ ,  $\alpha_{22} > \alpha_{12}$ ,  $x_1 \geq x_2$ ,
  - $\delta > 0$ ,  $\alpha_{22} > \alpha_{12}$ ,  $x_1 \leq 0$ ,
  - $\delta > 0$ ,  $\alpha_{22} < \alpha_{12}$ ,
  - $\delta < 0$ ,  $\alpha_{22} < \alpha_{12}$ ,  $x_1 \geq x_2$ ,
  - $\delta < 0$ ,  $\alpha_{22} < \alpha_{12}$ ,  $x_1 \leq 0$ ,
  - $\delta < 0$ ,  $\alpha_{22} < \alpha_{12}$ ,  $\Delta < 0$ ,

then  $l_3$  and  $l_4$  have no intersections in the first quadrant of the  $xz$  plane,

where  $\delta$  is defined in Proposition 2,

$$x_1 = \frac{d(\alpha_{22} + \beta)}{\alpha_{22}(sa - d\alpha) + d\beta\alpha_{21}}, \quad x_2 = \frac{\alpha_{22} - \alpha_{12}}{\delta},$$

$$\Delta = [\alpha_{22}(sa - d\alpha) + d\beta\alpha_{21} + \gamma r_1 s(\alpha_{12} - \alpha_{22})]^2 + 4d\delta\gamma r_1 s(\alpha_{22} + \beta)$$

and

$$x_2 < \frac{1}{\alpha_{21}} \text{ if } \alpha_{11} < \alpha_{21}.$$

The expressions of  $E_{xyz}$  and its stability criteria are too complex to be explicitly expressed in term of the parameters in (2.1). Theorem A.5 presents several cases when  $E_{xyz}$  exists. The deterministic nature of the model allows us to carry out a systematic numerical study with the help of Matlab software. Numerical simulations show that *A pisum*, *M viciae*, and *A ervi* can coexist together at the equilibrium

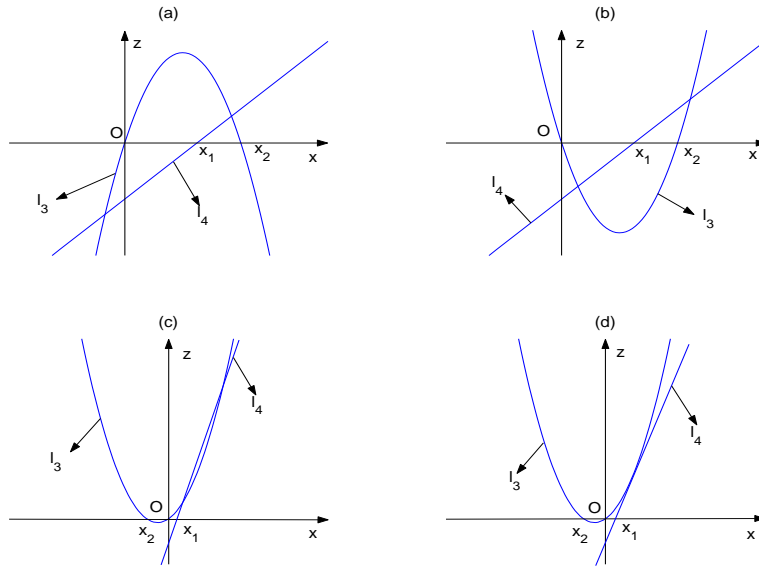


FIGURE A.5. (a)  $\delta > 0$ ,  $\alpha_{22} > \alpha_{12}$ ,  $0 < x_1 < x_2$ . (b)  $\delta < 0$ ,  $\alpha_{22} < \alpha_{12}$ ,  $0 < x_1 < x_2$ . (c)  $\delta < 0$ ,  $\alpha_{22} > \alpha_{12}$ ,  $\Delta > 0$ . (d)  $\delta < 0$ ,  $\alpha_{22} > \alpha_{12}$ ,  $\Delta = 0$

$E_{xyz}$  (see Fig. 3.1), where the values of parameters are chosen from Table 1.1. Fig. 3.2 shows other possible dynamics of (2.1).