

T. Nakazawa · N. Yamamura

## Community structure and stability analysis for intraguild interactions among host, parasitoid, and predator

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**Abstract** Intraguild predation (IGP) occurs when one species preys on a competitor species that shares a common resource. Modifying a prey–predator model with prey infection, we propose a model of IG interactions among host, parasitoid, and predator, in which the predator eats parasitized and unparasitized hosts, and the adult parasitoid density is explicitly expressed. Parameter dependences of community structure, including stability of the system, were analytically obtained. Depending on interaction strength (parasitization and predation on unparasitized and parasitized hosts), the model provides six types of community structure: (1) only the host exists, (2) the host and predator coexist stably, (3) the host and parasitoid coexist stably, (4) the host–parasitoid population dynamics are unstable, (5) the three species coexist stably, and (6) the population dynamics of the three species are unstable. In contrast to a traditional prey–predator model with prey infection, which predicts that population dynamics are always locally stable, our model predicts that they are unstable when the parasitization rate is high.

**Keywords** Aphid · Parasitoid wasp · Ladybird beetle system · Competitive exclusion · Insect community · Omnivory · Stage-structure

### Introduction

Intraguild predation (IGP) is predation by one competitor species on another that shares a common

resource. This type of interaction is widespread in nature (Arim and Marquet 2004). However, IGP has only recently become the subject of substantial empirical and theoretical research (Polis et al. 1989; Polis and Holt 1992; Holt and Polis 1997; McCann and Hastings 1997; Diehl 2003).

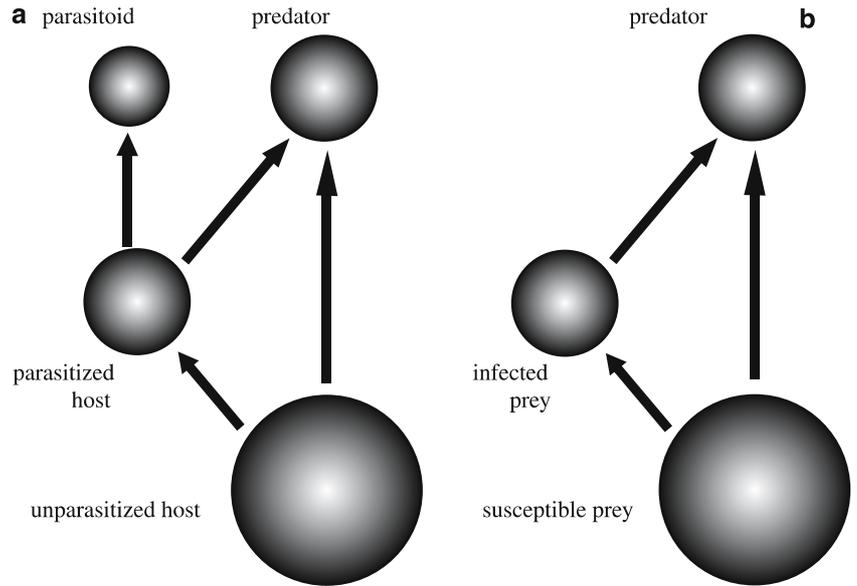
Here, we propose a model for IG interactions among host, parasitoid, and predator (Fig. 1a), as exemplified by the aphid, parasitoid wasp, and ladybird beetle system (Brodeur and Rosenheim 2000; Meyhöfer and Hindayana 2000; Wimp and Whitham 2001; Kaneko 2002, 2003a, b; Schmidt et al. 2003). In this system, the parasitoid (IG prey) lays eggs in the host, the predator (IG predator) consumes both unparasitized and parasitized hosts, and the parasitoid emerges from parasitized hosts that survive predation. This interaction constitutes IGP because the predator preys on the parasitoid by consuming parasitized hosts.

A number of models of prey–predator interactions with prey infection (Fig. 1b) have recently been proposed (Mukherjee 1998; Chattopadhyay and Arino 1999; Lenbury et al. 1999; Han and Ma 2001; Xiao and Chen 2001; Chattopadhyay and Pal 2002; Chattopadhyay et al. 2002, 2003; Hethcote et al. 2004; Singh et al. 2004; Hall et al. 2005). Traditional models have assumed that the IG prey is a parasitic species, such as a virus or parasite that spreads through direct contact between susceptible and infected prey, rather than a parasitoid with an independent adult phase. These traditional models may thus be misleading when applied to interactions among host, parasitoid, and predator, because adult parasitoids are usually not attacked by the predator, and IG prey variables are not explicitly represented.

Mylius et al. (2001) presented a useful model framework to address this problem. They developed a stage-structured IGP model for resource, consumer (IG prey), and predator (IG predator) interactions in which the adult consumer is invulnerable to predation. This model framework appears similar to the system of host, para-

T. Nakazawa (✉) · N. Yamamura  
Center for Ecological Research, Kyoto University,  
Kamitanakami-hirano-cho, Otsu 520-2113, Japan  
E-mail: nkzw@ecology.kyoto-u.ac.jp  
E-mail: yamamura@ecology.kyoto-u.ac.jp

**Fig. 1** Geometry of the interactions among **a** host, parasitoid, and predator and **b** prey and predator with prey infection



parasitoid, and predator, but differs in that juvenile consumers attack the resource and produce offspring, whereas in our system, juvenile parasitoids (in the host) do not.

Thus, we propose a model for IGP in host–parasitoid–predator systems (Fig. 1a) in which the adult parasitoid density is explicitly expressed and the parasitization rate depends on parasitoid density. Because of the incorporation of these variables, our model is necessarily more complex than previous models (compare Fig. 1a and b). The purpose of our study was to analyze this model to determine how it differs from traditional models (Fig. 1b).

Our model predicts various types of community structure depending on the parameter values. IGP can cause complex population dynamics, even when the community structure is very simple (Diehl 1995; Holt and Polis 1997). The relative strengths of direct and indirect interactions may strongly affect population dynamics (Bradley 1983; Polis et al. 1989). Consequently, we focused on the strengths of interactions (parasitization and predation), and examined the relationship between interaction strength and community structure. Finally, we compared the relationships obtained between interaction strength and community structure using two models (shown in Fig. 1) and discuss the differences between prey–predator models with prey infection and the host–parasitoid–predator model.

### Host–parasitoid–predator model

#### Equations and equilibria

We developed the following differential model for IG interactions among host, parasitoid, and predator:

$$\begin{aligned} \frac{dS(t)}{dt} &= r\left(1 - \frac{S(t)}{K}\right)S(t) - xS(t)I(t) - yS(t)Q(t), \\ \frac{dI(t)}{dt} &= xS(t)P(t) - hI(t) - zI(t)Q(t), \\ \frac{dP(t)}{dt} &= \lambda hI(t) - d_p P(t), \\ \frac{dQ(t)}{dt} &= \delta\{yS(t) + zI(t)\}Q(t) - d_q Q(t), \end{aligned} \quad (1)$$

where  $S$ ,  $I$ ,  $P$ , and  $Q$  are the densities of the unparasitized host, the parasitized host, the parasitoid, and the predator, respectively, and  $r$  and  $K$  are the intrinsic growth rate and carrying capacity, respectively, of the host. We assumed that the host is killed by parasitization, but the parasitized host exists until a predator consumes it or the parasitoid emerges. Thus, the parasitized host does not affect intra-species competition or contribute to reproduction. This type of parasitoid is called an idiobiont. Parameters  $x$ ,  $y$ , and  $z$  represent the efficiencies of parasitization, predation on the unparasitized host, and predation on the parasitized host, respectively. Parameter  $h$  is the emergence rate of the parasitoid, and the inverse ( $1/h$ ) indicates the average latent period during which the parasitoid remains within the host until emergence. Parameter  $\lambda$  is the number of parasitoids that emerge from an individual host, and  $\delta$  is the conversion rate for predator reproduction. Here, we set the conversion rates to be the same whether the predator consumes the unparasitized or parasitized host. Finally,  $d_p$  and  $d_q$  are the mortality rates of the parasitoid and predator, respectively (see Table 1 for a summary of these parameters).

In general, delay-differential equations have been used for host–parasitoid models to consider explicitly the duration of the juvenile parasitoid stage (reviewed by Nisbet 1997; Murdoch et al. 2003). However, we used an

**Table 1** The host–parasitoid–predator model

	Symbol	Definition
Populations	$S(t)$	Density of unparasitized host at time $t$
	$I(t)$	Density of parasitized host at time $t$
	$P(t)$	Density of parasitoid at time $t$
	$Q(t)$	Density of predator at time $t$
Parameters	$r$	Intrinsic growth rate of host
	$K$	Carrying capacity of host
	$x$	Parasitization rate
	$y$	Predation rate on unparasitized host
	$z$	Predation rate on parasitized host
	$h$	Emergence rate of parasitoid
	$\lambda$	Number of parasitoids from individual host
	$\delta$	Conversion rate for predator reproduction
	$d_p$	Mortality rate of parasitoid
	$d_q$	Mortality rate of predator
Equilibria	$E_1$	Host
	$E_2$	Host and parasitoid
	$E_3$	Host and predator
	$E_4$	Host, parasitoid, and predator
Regions	I	$E_1$ is stable
	II	$E_2$ is stable
	III	$E_3$ is stable
	IV	$E_4$ is stable
	iii	$E_3$ is unstable
	iv	$E_4$ is unstable

ordinary differential model that is the simplest standard assumption for different transient stages in epidemiology studies (Anderson and May 1992; Middelboe 2000), assuming the transient rate is constant. Consequently, this assumption facilitates analysis of the model and comparison with traditional prey–predator models with prey infection.

This model has four types of equilibria:  $E_1(S_1^*, 0, 0, 0)$ ,  $E_2(S_2^*, 0, 0, Q_2^*)$ ,  $E_3(S_2^*, I_3^*, P_3^*, 0)$  and  $E_4(S_4^*, I_4^*, P_4^*, Q_4^*)$ , where variables with asterisks are positive. At  $E_1$ , only the host exists and both of its enemies are excluded. At  $E_2$  or  $E_3$ , the parasitoid or predator is excluded, and the host coexists with the remaining enemy. At  $E_4$ , the three species coexist. The equilibrium densities are calculated as follows:

$$E_1(S_1^*, 0, 0, 0) = (K, 0, 0, 0), \quad (2a)$$

$$E_2(S_2^*, 0, 0, Q_2^*) = \left( \frac{d_q}{y\delta}, 0, 0, \frac{r}{Ky}(K - S_2^*) \right) \quad (2b)$$

$$E_3(S_3^*, I_3^*, P_3^*, 0) = \left( \frac{d_p}{x\lambda}, \frac{r}{Kh}S_3^*(K - S_3^*), \frac{h\lambda}{d_p}I_3^*, 0 \right), \quad (2c)$$

and

$$E_4(S_4^*, I_4^*, P_4^*, Q_4^*) = \left( K \left\{ 1 - \frac{hy}{rzS_3^*} (S_2^* - S_3^*) \right\}, \frac{y}{z} (S_2^* - S_4^*), \frac{h\lambda}{d_p} I_4^*, \frac{h}{zS_3^*} (S_4^* - S_3^*) \right). \quad (2d)$$

## Existence and local stability of equilibria

We examined conditions under which each equilibrium exists and is locally stable (see Appendix A for analyses). For  $E_1$  to be locally stable,

$$y < \frac{d_q}{K\delta}, \quad (3a)$$

and

$$x < \frac{d_p}{K\lambda}. \quad (3b)$$

Thus, when inequalities 3a and b are both satisfied,  $E_1$ , in which only the host is present, is stable; otherwise, this equilibrium is unstable.

For  $E_2$  to be stable,

$$y > \frac{d_q}{K\delta}, \quad (4a)$$

and

$$z > \frac{Khy(d_q\lambda x - d_p\delta y)}{rd_p(K\delta y - d_q)}. \quad (4b)$$

When inequalities 4a and b are satisfied,  $E_2$ , in which the parasitoid is excluded and the host and predator coexist, is stable.

For  $E_3$  to be stable,

$$z < \frac{Kh\lambda x(d_q\lambda x - d_p\delta y)}{rd_p\delta(K\lambda x - d_p)}, \quad (5a)$$

$$x > \frac{d_p}{K\lambda} \quad (5b)$$

and

$$x < \frac{X + \sqrt{X^2 + 4rhd_p(d_p + h)}}{2Kh\lambda}, \quad (5c)$$

where  $X = (d_p + h)^2 + d_ph$ . When inequalities 5a–c are satisfied,  $E_3$ , in which the predator is excluded and the host and parasitoid coexist, is stable. When Eq. 5a and b are satisfied but Eq. 5c is not, the equilibrium with only the host and parasitoid present is unstable.

For  $E_4$  to be stable,

$$\frac{d_p}{x\lambda} < \frac{d_q}{y\delta}, \quad (6a)$$

$$\frac{rd_p(K\delta y - d_q)}{Khy(d_q\lambda x - d_p\delta y)} < \frac{1}{z} < \frac{rd_p\delta(K\lambda x - d_p)}{Kh\lambda x(d_q\lambda x - d_p\delta y)}, \quad (6b)$$

and

$$a_1 a_2 a_3 - a_3^2 - a_1^2 a_4 > 0, \quad (6c)$$

where  $a_i$  ( $i=1-4$ ) is shown in Eq. 16a–d (Appendix A). Inequality 6c is very complex to express directly using the original parameters, but can be expressed using Eqs. 2a–d and 16a–d to give the condition under which  $E_4$  is locally stable. When 6a and b are satisfied, but 6c is

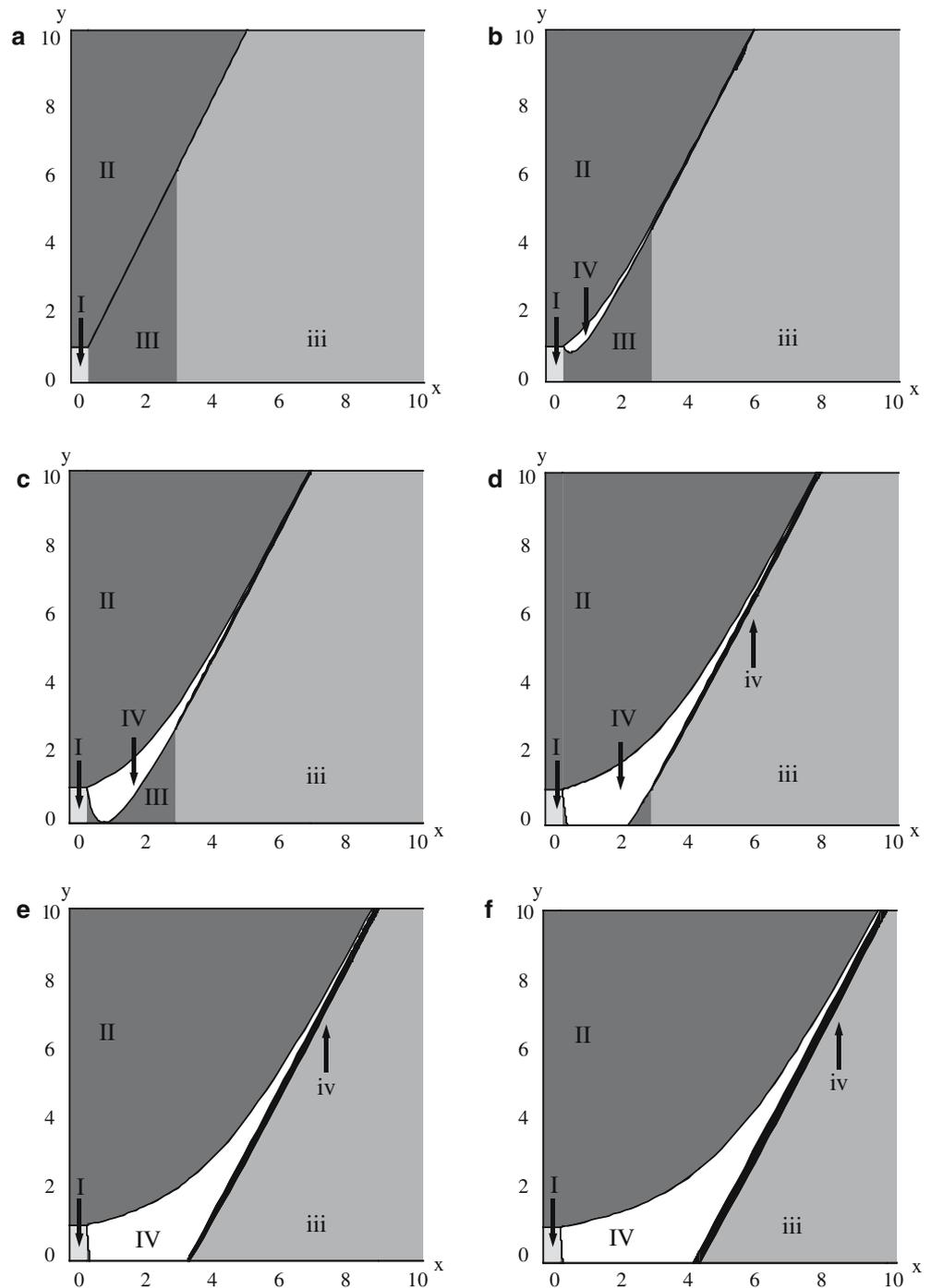
not, the equilibrium in which the three species are present is unstable.

### Relationships between interaction strength and community structure

From inequalities 3a, b to 6a–c, we obtained the relationship between interaction strength and community

structure and represented the numerically calculated results in parameter space (Fig. 2). Referring to Holt and Polis (1997), we set the default parameters as  $r=1$ ,  $K=1$ ,  $h=1$ ,  $\lambda=1$ ,  $\delta=0.5$ ,  $d_p=0.5$ , and  $d_q=0.5$ . After analysis of the model using this default parameter set, we examined how the results changed with alteration of the parameter values. In each panel of Fig. 2, the horizontal and vertical axes represent the parasitization rate ( $x$ ) and the predation rate on the unparasitized host ( $y$ ) for

**Fig. 2a–f** Relationship between interaction strength (parasitization rate  $x$  and predation rate on the unparasitized host  $y$ ) and community structure for various strengths of predation on the parasitized host ( $z$ ). **a**  $z=0$ , **b**  $z=2$ , **c**  $z=4$ , **d**  $z=6$ , **e**  $z=8$ , and **f**  $z=10$ . In each panel, the *horizontal* and *vertical axes* represent the parasitization rate ( $x$ ) and the predation rate on the unparasitized host ( $y$ ), respectively. In region *I*, only the host persists. In regions *II* and *III*, the predator or the parasitoid coexists with the host in a stable equilibrium. In region *iii*, the population dynamics between the host and parasitoid are unstable. In region *IV*, the three species coexist in a stable equilibrium. In region *iv*, the population dynamics among the three species are unstable



various rates of predation on the parasitized host ( $z$ ). The parameter space is divided into six mutually exclusive regions (I–IV, iii, and iv) depending on interaction strength.

$E_1$  is locally stable in region I within an area where both the parasitization rate ( $x$ ) and the predation rate on the unparasitized host ( $y$ ) are low, i.e., the conditions described by inequalities 3a, b. In this region, when both enemies are inefficient in exploiting the host, they are both excluded and only the host exists.

$E_2$  is locally stable in region II, where the parasitization rate ( $x$ ) is low and the predation rates on both the unparasitized host ( $y$ ) and parasitized host ( $z$ ) are high, i.e., the conditions described by 4a, b. In this region, when the predator is more efficient than the parasitoid, the parasitoid is excluded and the host and predator coexist.

$E_3$  is locally stable in region III, where the parasitization rate ( $x$ ) is moderate and the predation rates on both the unparasitized host ( $y$ ) and parasitized host ( $z$ ) are low, i.e., the conditions described by 5a–c. In this region, when the parasitoid is moderately more efficient than the predator, the predator is excluded and the host and parasitoid coexist. When the parasitization rate ( $x$ ) is too high and inequality 5c does not apply,  $E_3$  becomes unstable and the system shifts into region iii. In this region, a host–parasitoid limit cycle occurs (Fig. 3a). Region iii also narrows as the predation rate on the parasitized host ( $z$ ) increases.

$E_4$  is locally stable in region IV, where the parasitization rate ( $x$ ) is moderate, the predation rate on the unparasitized host ( $y$ ) is low, and the predation rate on the parasitized host ( $z$ ) is high, i.e., the conditions de-

scribed by 6a–c. In this region, the parasitoid uses the host moderately, and the predator attacks the parasitized host more efficiently than it attacks the unparasitized host. From a different viewpoint, if the predation rate on the parasitized host ( $z$ ) is assumed to represent the IGP level, the model suggests that the three species are more likely to coexist when the IGP level is higher, and the three species do not coexist when  $z=0$ . When the parasitization rate ( $x$ ) is slightly higher and inequality 6c no longer applies,  $E_4$  becomes unstable and the system shifts into region iv. In this region, a three-species limit cycle occurs (Fig. 3b). Region IV is sandwiched between two divided portions of region III when  $y$  is low and  $z$  is moderate (Fig. 2c and d), i.e., when the predator population is sustained by depending mainly on the parasitized host. In this situation, the predator is excluded from coexistence with the other species as the parasitization rate ( $x$ ) increases, and the system shifts to the right, from region IV into region III, by competitive exclusion. In contrast, the predator is excluded as the parasitization rate ( $x$ ) decreases, shifting the system to the left, from region IV into region III, because the predator is pushed to extinction owing to a shortage of the resource, the parasitized host.

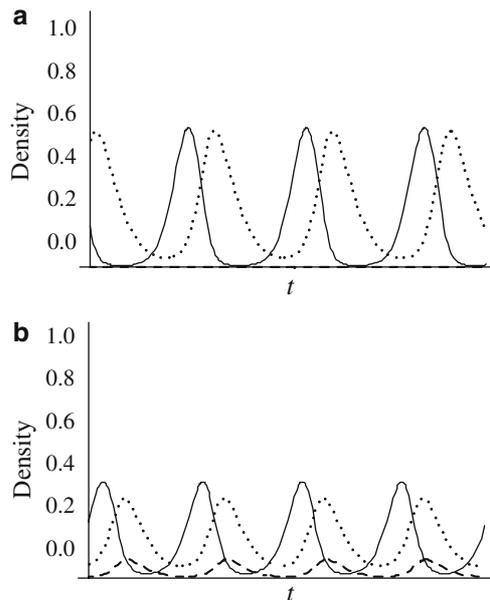
We conducted numerical calculations to test global stability, varying the initial population densities. When the equilibria are locally stable in regions I, II, III, and IV, they are always globally stable; when the equilibria are unstable in regions iii and iv, the densities do not change chaotically, but approach limit cycles (Fig. 3). Because all regions are mutually exclusive, there were no cases in which more than two attractors coexisted.

### Parameter effects

In this section, we briefly describe the parameter effects on boundary conditions in Eqs. 3a, b to 6a–6c (see Appendix B for details). We obtained the natural results that the parasitoid is better at invading the host population (3b) or the host–predator system (4b) when it performs well (high growth rate or low mortality rate). Similar results were obtained for the predator (3a and 5a).

Resource condition has opposite effects on the invasibility of the parasitoid or predator into the systems of the host and the other enemy. The predator is more likely to invade the host–parasitoid system with an increase in host-carrying capacity ( $K$ ) (5a), but the parasitoid is less likely to invade the host–predator system under this condition (4b). This result suggests that the three species are most likely to coexist at an intermediate level of productivity. This pattern was also suggested in previous studies of the IGP model (Holt and Polis 1997; Mylius et al. 2001).

The host–parasitoid system is more likely to be unstable when the parasitoid performs well (high growth rate or low mortality rate) (5c). Inequality 6c represents the boundary between regions IV and iv, i.e., the



**Fig. 3** Limit cycles of **a** the host and parasitoid in region iii and **b** the three species in region iv. Solid, dotted, and broken lines represent the densities of the host, parasitoid, and predator, respectively. **a**  $(x, y, z) = (1, 1, 4)$  and **b**  $(x, y, z) = (5, 4, 6)$

required condition for stability of the three-species system. Shifts in this boundary are difficult to predict because of the complexity of this inequality. However, this boundary would be expected to have shifts almost parallel to those between regions iii and iv because region iv is usually very narrow.

### Prey-predator model with prey infection

In model 1, the parasitization rate depends on adult parasitoid density. We changed this assumption to represent a contagion process, which is the assumption in traditional prey-predator models with prey infection (Fig. 1b). Replacing  $xS(t)$   $P(t)$  in model (1) with  $xS(t)$   $I(t)$  and omitting the variable  $P(t)$ , we obtain the following equations:

$$\begin{aligned}\frac{dS(t)}{dt} &= r\left(1 - \frac{S(t)}{K}\right)S(t) - xS(t)I(t) - yS(t)Q(t), \\ \frac{dI(t)}{dt} &= xS(t)I(t) - hI(t) - zI(t)Q(t), \\ \frac{dQ(t)}{dt} &= \delta\{yS(t) + zI(t)\}Q(t) - d_qQ(t).\end{aligned}\quad (7)$$

This model framework is the same as that of the IGP model proposed by Holt and Polis (1997). Here, we present results obtained from our model 1 compared to results from the traditional model 7. In model 7,  $S$ ,  $I$ , and  $Q$  are the densities of susceptible prey, infected prey, and the predator, respectively. Parameters  $x$ ,  $y$ , and  $z$  represent the efficiencies of infection, predation on susceptible prey, and predation on infected prey, respectively. Parameter  $h$  corresponds to the mortality rate caused by infection in the traditional model, whereas it corresponds to the emergence rate of the parasitoid in our model 1. In both cases, it represents loss rate  $I(t)$  by causes other than predation. The other parameters are defined as in our model, described by model 1. In model 7, the variables of the actual IG prey, which is a virus or parasite, are not explicitly expressed for simplicity. The assumption here is that the IG prey diffuses through contagion, and the infection rate depends on the infected prey density.

Model 7 also has four types of equilibria:  $E_1(S_1^*, 0, 0)$ ,  $E_2(S_2^*, 0, Q_2^*)$ ,  $E_3(S_2^*, I_3^*, 0)$ , and  $E_4(S_4^*, I_4^*, Q_4^*)$ . Their equilibrium densities are as follows:

$$E_1(S_1^*, 0, 0) = (K, 0, 0), \quad (8a)$$

$$E_2(S_2^*, 0, Q_2^*) = \left(\frac{d_q}{y\delta}, 0, \frac{r}{Ky}(K - S_2^*)\right), \quad (8b)$$

$$E_3(S_3^*, I_3^*, 0) = \left(\frac{h}{x}, \frac{r}{Kx}(K - S_3^*), 0\right), \quad (8c)$$

and

$$E_4(S_4^*, I_4^*, Q_4^*) = \left(K\left\{1 - \frac{xy}{rz}(S_2^* - S_3^*)\right\}, \frac{y}{z}(S_2^* - S_4^*), \frac{x}{z}(S_4^* - S_3^*)\right). \quad (8d)$$

Using the same analytical process as that applied to our model 1, we obtained the following required conditions for equilibria  $E_1$ – $E_4$  to be locally stable:

$$x < \frac{h}{K} \text{ and } y < \frac{d_q}{K\delta}, \quad (9a)$$

$$y > \frac{d_q}{K\delta} \text{ and } z > \frac{Ky(d_qx - h\delta y)}{r(K\delta y - d_q)}, \quad (9b)$$

$$x > \frac{h}{K} \text{ and } z < \frac{Kx(d_qx - h\delta y)}{r\delta(Kx - h)}, \quad (9c)$$

and

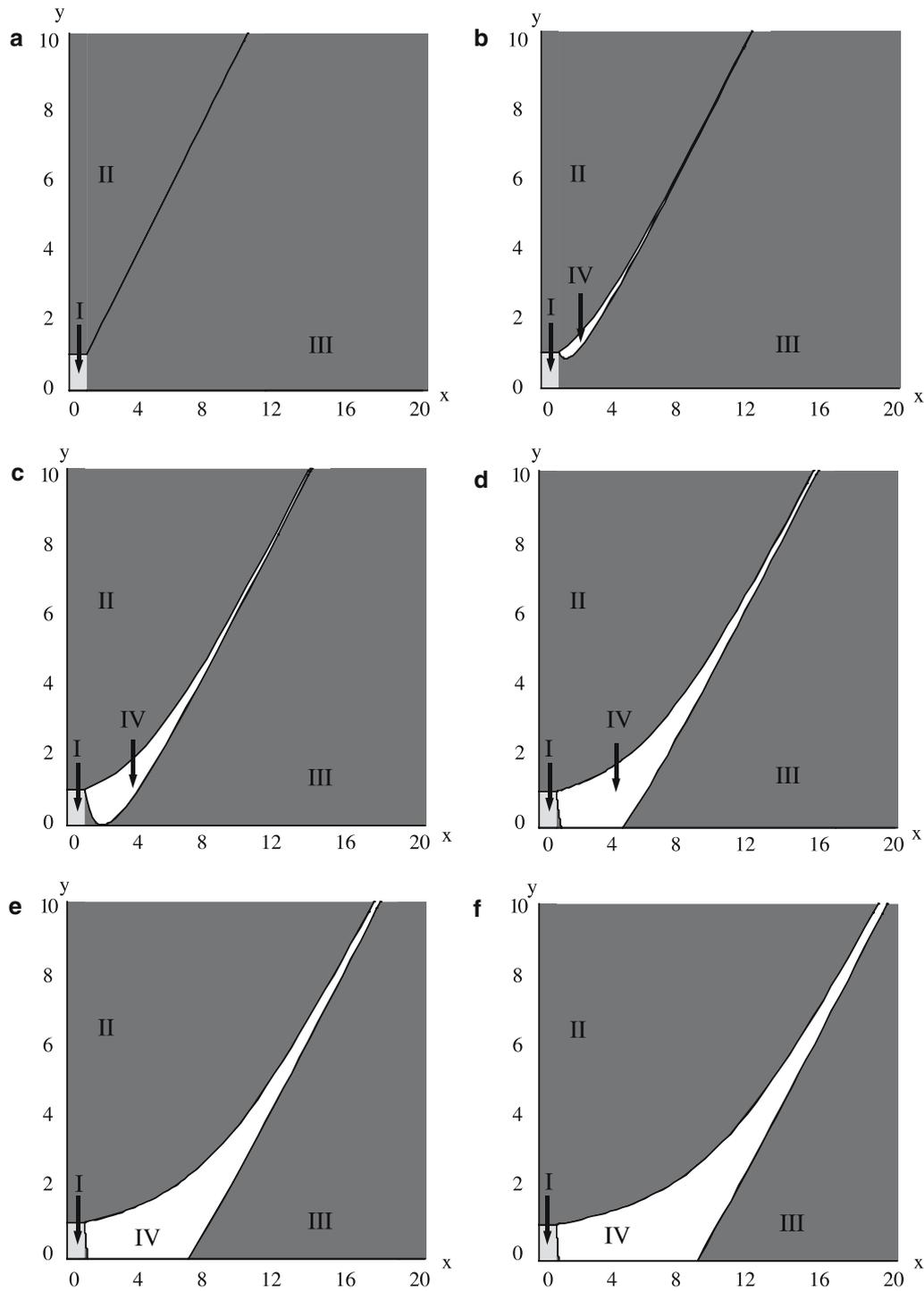
$$\frac{h}{x} < \frac{d_q}{y\delta} \text{ and } \frac{r(K\delta y - d_q)}{Ky(d_qx - h\delta y)} < \frac{1}{z} < \frac{r\delta(Kx - h)}{Kx(d_qx - h\delta y)}. \quad (9d)$$

From the above conditions and using the default parameter values, we calculated the relationships between interaction strength and community structure (Fig. 4). For surviving species, the resulting pattern of community structure is similar to that obtained using our model 1: the prey exists alone without infection when both infection and predation rates are low (region I); the prey and predator coexist stably without infection when the predation rate is high and the infection rate is low (region II); the prey exists alone with infection when the infection rate is high and the predation rate is low (region III); and the prey and predator coexist stably with infection when the infection rate is moderate and the predation rate of susceptible prey is low and that of infected prey is high (region IV).

However, the two models differ in their predictions of stability, particularly in the parameter space where the infection rate is high. The traditional model indicates locally stable equilibria in regions III and IV, whereas our model indicates the existence of host-parasitoid or three-species limit cycles in regions iii and iv (Figs. 2 and 4). This difference is apparently attributable to time-delayed interactions between the host and parasitoid that are incorporated into our model, but are absent from the traditional model 7.

### Discussion

We proposed and analyzed a model for IG interactions among a host, a parasitoid, and a predator (Fig. 1a), as exemplified by the aphid, parasitoid wasp, and ladybird beetle system (Brodeur and Rosenheim 2000; Meyhöfer and Hindayana 2000; Wimp and Whitham 2001; Kaneko 2002, 2003a, b; Schmidt et al. 2003). In this system, the parasitoid lays eggs in the host, the predator attacks both the unparasitized and parasitized hosts, and the parasitoid emerges from parasitized hosts that survive predation. This model may also be applied to aquatic ecosystems in which viruses suspended in the water are analogous to parasitoids in insect communities



**Fig. 4a–f** Relationship between interaction strength (infection rate  $x$  and predation rate on the susceptible prey  $y$ ) and community structure for various strengths of predation on the infected prey. **a**  $z=0$ , **b**  $z=2$ , **c**  $z=4$ , **d**  $z=6$ , **e**  $z=8$ , and **f**  $z=10$ . In regions *I*

and *II*, the prey exists alone or coexists stably with the predator without prey infection. In regions *III* and *IV*, the prey exists alone or coexists stably with the predator with prey infection

(Suttle and Chen 1992; González and Suttle 1993; Manage et al. 2002).

Our model predicted six types of population dynamics depending on the strength of species interactions (Fig. 2). Viewing these predicted patterns should be useful when examining communities in which three interaction

strengths are dependent on several variables. For example, the community structure of the system composed of aphids, parasitoid wasps, and ladybird beetles varies depending on the existence and activity of ants that have a mutualistic relationship with aphids (Wimp and Whitham 2001; Kaneko 2002, 2003a, b). For example,

when  $(x, y, z) = (4, 2, 8)$ , our model predicts that the three species will coexist stably (Fig. 2e). However, if the predation rate decreases because of a certain factor, such as ant attendance, and  $(x, y, z) = (4, 1, 4)$ , an unstable host–parasitoid system results (Fig. 2c).

Many researchers have used prey–predator models with prey infection when considering IGP systems in which the IG prey is a parasitic species (Fig. 1b). In the traditional models, the density of IG prey was not directly represented because of the assumption that infection is caused by contagion between susceptible and infected prey. Consequently, these models are less complex and easier to manipulate than our model. The traditional model is certainly appropriate for analysis of IGP systems in which a parasitic IG prey diffuses through contagion, but may not be optimal for analysis of IGP interactions among host, parasitoid, and predator. Our results confirm that the two models are qualitatively similar in that the community structure depends on the three interaction strengths, and both models indicate that the coexistence of the three species is influenced by IG interactions. This is contrary to our expectation that the community structure pattern would drastically change with additional stage structure. However, the two models differ substantially in that the traditional model predicts the existence of stable equilibria in the parameter spaces where limit cycles are predicted by our model (Fig. 3). When predicting population dynamics in practical applications, this quantitative difference is crucial, even if the two models predict the same species composition under a given condition. Therefore, it is important to distinguish between the applicability of the two models, depending on whether the infection process is parasitization or contagion.

The difference between our model and the traditional prey–predator model with prey infection is attributable to a consideration of the stage structure of the parasitoid; parasitoids have both a free-living adult stage and a host-dependent larval stage. We modeled this system in the simplest way possible by assuming that the adult parasitoid emerges from parasitized hosts at a constant rate.

A more realistic and interesting exercise would be to analyze a delay-differential model, which is a type of model commonly used to represent host–parasitoid interactions (reviewed by Nisbet 1997; Murdoch et al. 2003). We would obtain different results using delay-differential equations: unstable equilibria would be more likely and the parameter dependence of community structure could change. Furthermore, a different type of population cycle would arise in some parameter spaces, which may be caused by the explicit consideration of the developmental time lag of the parasitoid. Further analyses are required to understand these consequences.

Mylius et al. (2001) explored a stage-structured IGP model to evaluate resource, consumer (IG prey), and predator (IG predator) interactions. They incorporated stage structure into the consumer and found that the invulnerable adult stage affected community structure.

According to their results, the adult stage is a refuge from predation for the IG prey, which then becomes more likely to maintain its population. However, the equilibria were always locally stable, contrary to our results. In their model, the juvenile IG prey attacks the resource and produces offspring, whereas it does not in our model because we assumed host–parasitoid interaction (the parasitoid in the host does not attack other hosts). This difference in the assumptions of the two models creates an essential difference in the stability of the system. The two models also differ in linearity among species interactions. Introducing non-linearity may lead to alternative stable states (Holt and Polis 1997). If a type-II function is assumed in our model, as in Mylius et al. (2001), we will obtain similar bistability at intermediate productivity, but the equilibria would be unstable for some parameter range.

In general, incorporating stage structure that is a refuge from predation has a stabilizing effect on population dynamics (e.g., MacNair 1987). However, we showed that the refuge had a destabilizing effect, which is in marked contrast to previous studies. The destabilizing effect occurred because the host–parasitoid interaction involves a time lag before the parasitoid emerges from the parasitized host after the parasitoid egg is laid. However, the instability would be weakened if the vulnerable juveniles reproduced by attacking the resource, because the time lag between birth and reproduction would be reduced. This type of interaction would stabilize the system of traditional prey–predator models with prey infection (Fig. 1b) and the system described by Mylius et al. (2001).

Researchers have used stage-structured models to model insect communities. Therefore, the stage structure of both the host and predator should also be considered in our model, because natural insect communities include species with various types of life history, and a number of previous models have shown that stage structure has a large effect on the results (reviewed by Murdoch et al. 2003). For example, different parasitoids may attack different developmental stages of the same host (Briggs 1993; Briggs et al. 1993; see also Haigh and Maynard Smith 1972; May and Hassell 1981). Some parasitoids (hyperparasitoids) may attack hosts that have been parasitized by other parasitoids (May and Hassell 1981; Briggs 1993). However, no researchers have rigorously explored a model for the IG interaction among host, parasitoid, and predator, although this interaction is widespread among insect communities. Therefore, it will be necessary to extend the present model to advance our understanding of the dynamics of natural insect communities.

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## Appendix A

### Existence and local stability of equilibria

Here, we show the details of the mathematical analyses to obtain the parameter conditions for Eqs. 3a, b to 6a–6c. The characteristic equation for  $E_1$  is  $(A+r)(A-y\delta S_1^*+d_q)(A^2+a_1A+a_2)$  ( $A$  is the eigenvalue), where

$$a_1 = h + d_p, \quad (10a)$$

and

$$a_2 = h(d_p - x\lambda S_1^*). \quad (10b)$$

$E_1$  is locally stable when the real parts of the roots of the characteristic equation are all negative. Because  $r$  and  $a_1$  are always positive, it is required that  $y\delta S_1^* - d_q < 0$  and  $a_2 > 0$ . These inequalities provide the following conditions:

$$y < \frac{d_q}{K\delta}, \quad (11a)$$

and

$$x < \frac{d_p}{K\lambda}. \quad (11b)$$

The characteristic equation for  $E_2$  is  $(A^2 + a_1A + a_2)(A^2 + a_3A + a_4) = 0$ , where

$$a_1 = \frac{r}{K}S_2^*, \quad (12a)$$

$$a_2 = y^2\delta S_2^*Q_2^*, \quad (12b)$$

$$a_3 = zQ_2^* + d_p + h, \quad (12c)$$

and

$$a_4 = d_p(zQ_2^* + h) - hx\lambda S_2^*. \quad (12d)$$

Therefore,  $E_2$  is locally stable when  $a_i > 0$  ( $i=1-4$ ). From Eq. (2b),  $S_2^*$  is always positive and  $Q_2^*$  is positive when

$$y > \frac{d_q}{K\delta}. \quad (13a)$$

Under these conditions,  $a_i > 0$  ( $i=1-3$ ). Another condition,  $a_4 > 0$ , provides that

$$z > \frac{Khy(d_q\lambda x - d_p\delta y)}{rd_p(K\delta y - d_q)}. \quad (13b)$$

The characteristic equation for  $E_3$  is  $(A - y\delta S_3^* - z\delta I^* + d_q)(A^3 + a_1A^2 + a_2A + a_3) = 0$ , where

$$a_1 = \frac{r}{K}S_3^* + d_p + h, \quad (14a)$$

$$a_2 = \frac{r(d_p + h)}{K}S_3^*, \quad (14b)$$

and

$$a_3 = \frac{rd_ph}{K}(K - S_3^*). \quad (14c)$$

The first requirement for the local stability of  $E_3$  is  $y\delta S_3^* + z\delta I^* - d_q < 0$ , and therefore,

$$z < \frac{Kh\lambda x(d_q\lambda x - d_p\delta y)}{rd_p\delta(K\lambda x - d_p)}. \quad (15a)$$

From the Routh-Hurwitz criteria, it is also necessary that  $a_i > 0$  ( $i=1-3$ ) and  $a_1a_2 - a_3 > 0$ . Because equilibrium densities should be positive,  $a_i > 0$  ( $i=1-3$ ). From Eq. 2c,  $K - S_3^* > 0$  is equivalent to

$$x > \frac{d_p}{K\lambda}. \quad (15b)$$

Moreover,  $a_1a_2 - a_3 > 0$  provides

$$x < \frac{X + \sqrt{X^2 + 4rhd_p(d_p + h)}}{2Kh\lambda} \quad (15c)$$

where  $X = (d_p + h)^2 + d_ph$ .

Finally, the characteristic equation for  $E_4$  is  $A^4 + a_1A^3 + a_2A^2 + a_3A + a_4 = 0$ , where

$$a_1 = d_p + \frac{r}{K}S_4^* + h\frac{S_4^*}{S_3^*}, \quad (16a)$$

$$a_2 = \frac{r}{K}S_4^* \left( d_p + h\frac{S_4^*}{S_3^*} \right) + \delta(y^2S_4^* + z^2I_4^*)Q_4^*, \quad (16b)$$

$$a_3 = \frac{r}{K}\delta z^2S_4^*I_4^*Q_4^* + d_p\delta(y^2S_4^* + z^2I_4^*)Q_4^* + h\frac{S_4^*}{S_3^*}(d_pxP_4^* + d_qyQ_4^*), \quad (16c)$$

and

$$a_4 = \frac{r}{K}d_p\delta z^2S_4^*I_4^*Q_4^*. \quad (16d)$$

From the Routh-Hurwitz criteria,  $E_4$  is locally stable when  $a_i > 0$  ( $i=1-4$ ),  $a_1a_2 - a_3 > 0$ , and  $a_1a_2a_3 - a_3^2 - a_1^2a_4 > 0$ . As  $a_1a_2a_3 - a_3^2 - a_1^2a_4 > 0$  satisfies  $a_1a_2 - a_3 > 0$  when  $a_i > 0$  ( $i=1-4$ ), the condition  $a_1a_2 - a_3 > 0$  need not be examined because equilibrium densities should be positive, i.e.,  $a_i > 0$  ( $i=1-4$ ). From Eq. 2d, the condition for positive equilibrium densities is

$$\frac{rd_p(K\delta y - d_q)}{Khy(d_q\lambda x - d_p\delta y)} < \frac{1}{z} < \frac{rd_p\delta(K\lambda x - d_p)}{Kh\lambda x(d_q\lambda x - d_p\delta y)}. \quad (17a)$$

$$\frac{d_p}{x\lambda} < \frac{d_q}{y\delta}. \quad (17b)$$

The rest condition is

$$a_1a_2a_3 - a_3^2 - a_1^2a_4 > 0. \quad (17c)$$

## Appendix B

### Parameter effects

We considered the effects of the parameters on the boundary conditions described by inequalities 3a, b to 6a–c. First, inequalities 3a and 4a represent the boundary between regions I and II, that is, the required conditions for the predator to invade the host population. This threshold decreases when the predator has a higher fecundity ( $\lambda$ ) or a lower mortality rate ( $d_p$ ), indicating that the predator is more likely to persist when its potential population growth rate is high. Because a host with a large carrying capacity ( $K$ ) should facilitate sustaining the parasitoid population, this threshold decreases with increasing  $K$ .

Inequalities 5a and 6a represent the boundaries between regions III and IV and between iii and iv, respectively; these represent the required conditions for invasion of the host–parasitoid system by the predator. The threshold decreases and regions III and iii are reduced when the predator has a higher fecundity ( $\lambda$ ) or a lower mortality rate ( $d_p$ ), indicating that the predator is more likely to persist when its potential population growth rate is high. The threshold also decreases when the potential parasitoid growth rate is low, i.e., when the parasitoid has a lower fecundity ( $\delta$ ), a higher mortality rate ( $d_q$ ), or a longer latent period ( $1/h$ ). Increases in potential host growth rate ( $r$  or  $K$ ) also decrease this threshold, suggesting that the predator is more likely to persist when the resource is abundant. In general, when the predator is relatively more efficient in its growth than the parasitoid, this boundary shifts downward in Fig. 2, indicating that the predator would be more likely to invade the host–parasitoid system.

Inequality 3b represents the boundary between regions I and III, i.e., the required condition for invasion of the host population by the parasitoid. This boundary exhibits a similar pattern of shifts to that exhibited by the boundary between regions I and II. This threshold decreases with increases in potential parasitoid growth rate (higher  $\lambda$  or lower  $d_p$ ) and with increasing host carrying capacity ( $K$ ), suggesting that the parasitoid is more likely to invade the host population when its growth is efficient or the resource is in good condition.

Inequality 4b represents the boundary between regions II and IV, i.e., the required condition for invasion of the host–predator system by the parasitoid. This boundary exhibits a contrasting pattern of shifts to that exhibited by the boundaries between regions III and IV and between iii and iv. This threshold increases with increasing potential parasitoid growth rate (higher  $\lambda$ , lower  $d_p$ , or higher  $h$ ) and decreases with decreasing potential predator growth rate (lower  $\delta$  or higher  $d_q$ ), suggesting that when the growth potential of the parasitoid is relatively more efficient than that of the

predator, the boundary shifts upward in Fig. 2, indicating that the parasitoid would be more likely to persist. Moreover, this threshold decreases with increasing host growth rate ( $r$  or  $K$ ), suggesting that the parasitoid is more likely to be excluded from the three-species system when the resource is abundant.

Inequality 5c represents the boundary between regions III and iii, i.e., the required condition for the host–parasitoid system to be stable, suggesting that the system is more likely to be stable when the parasitoid has a low fecundity ( $\lambda$ ) or a high mortality rate ( $d_p$ ). The dependency of stability on  $h$  is complex because this threshold is a unimodal function of  $h$ . While increasing the latent period ( $1/h$ ) has a stabilizing effect,  $E_3$  is more likely to be stable when the latent period is extremely short, indicating that short latent periods eliminate the time delay in host–parasitoid interactions.

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