

# The role of transient dynamics in biological pest control: insights from a host–parasitoid community

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## Summary

1. Identifying natural enemies that can maintain pests at low abundances is a priority in biological control. Here, we show that experiments combined with models generate new insights into identifying effective control agents prior to their release in the field. Using a host–parasitoid community (the harlequin bug and its egg parasitoids) as a model system, we report three key findings.

2. The interplay between the host's self-limitation and the parasitoids' saturating functional response causes the long-term (steady-state) outcomes for pest suppression to differ from those of short-term (transient) dynamics. When the bug's self-limitation is moderately strong, the parasitoid with the higher attack rate and conversion efficiency (*Ooencyrtus*) achieves greater host suppression in the long term, but its longer handling time causes long periods of transient dynamics during which the bug can reach high abundances; when the bug's self-limitation is weak, host fluctuations amplify over time and *Ooencyrtus* fails at host suppression altogether. In contrast, the parasitoid with the lower attack rate and conversion efficiency but the shorter handling time (*Trissolcus*) induces only weak transient fluctuations of short duration and can maintain the host at low abundances regardless of the strength of the bug's self-limitation.

3. Release of multiple enemy species can compromise host suppression if an enemy that induces stronger transient fluctuations excludes one that induces weaker fluctuations. For instance, *Ooencyrtus* excludes *Trissolcus* despite having a longer handling time because of its higher conversion efficiency. The model correctly predicts the time to exclusion observed in experiments, suggesting that it captures the key biological features of the host–parasitoid interaction.

4. Intraspecific interference reduces long-term pest suppression but improves short-term pest control by reducing the magnitude and duration of transient fluctuations.

5. These results highlight the importance of transient dynamics in pest suppression. Pests are unlikely to be strongly self-limited because they attack crop monocultures. Hence, pest fluctuations are likely to dominate short-term dynamics even when the long-term outcome is a stable equilibrium. The tendency to induce strong transient fluctuations (e.g. through a long handling time) is therefore a crucial consideration when identifying effective pest control agents.

**Key-words:** attack rate, biological control, functional response, handling time, pest–enemy, transient dynamics

## Introduction

The success of biological control hinges on the ability to identify effective control agents prior to releasing them in the field. The typical approach in evaluating natural enemy agents is to quantify attack rates and handling times by measuring functional responses (e.g. Dixon 2000; Bezemer & Mills 2001; Gitonga *et al.* 2002; Fernandez-arhex & Corley 2003; Lee & Kang 2004; Rutledge & O'Neill 2005; Seko & Miura 2008; Britto *et al.* 2009). Attack rates and handling times are useful

indicators of an enemy species' efficiency at exploiting a pest (Hassell 1978; Ehler 1990; Waage 1990; Murdoch 1990, 1992; Waage & Mills 1992). However, these parameters in themselves do not inform us about the population-level effects of natural enemies, in particular, the degree of pest suppression and the stability of the pest–enemy interaction. To predict pest suppression and stability, we need to know the numerical response (per capita growth rate) of the natural enemy, which involves the functional response as well as the conversion efficiency and background mortality. The numerical response is also critical in determining the nature of the interactions between multiple natural enemies (Godfray & Waage 1991; Murdoch, Briggs & Nisbet 1996). An enemy species with a

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high attack rate and short handling time may be excluded by an enemy species with a comparable attack rate but a longer handling time if the latter has a higher conversion efficiency.

When determining whether a given natural enemy can maintain a stable, long-term interaction with the pest, it is crucial to keep in mind that pests are unlikely to be strongly self-limited given that they typically attack large monocultures of crops that present little resource limitation. Because most natural enemies exhibit saturating (Type II) functional responses (Holling 1959a,b), fluctuations in pest and enemy abundances driven by the functional response are likely to dominate short-term dynamics even when the long-term outcome is a stable equilibrium. An enemy species with a high attack rate and conversion efficiency but a long handling time is more likely to cause strong fluctuations in pest–enemy abundances than a species with a lower attack rate and conversion efficiency but a shorter handling time. These considerations make it important to elucidate both the transient dynamics of a given enemy's interaction with the pest and the long-term, steady-state outcomes. Knowing this information in advance is critical in determining which natural enemy species should be released in the field. Although a large number of studies have investigated transient dynamics in plant and animal populations (e.g. Bierzychudek 1999; Clutton-Brock & Coulson 2002; Coulson, Guinness, Pemberton & Clutton-Brock 2004; Koons, Grand, Zinner & Rockwell 2005; Koons, Holmes & Grand 2007; Ozgul *et al.* 2009; Tenhumberg, Tyre & Rebarber 2009), no study to date has investigated the role of transient fluctuations in pest–enemy dynamics.

Here, we combine laboratory experiments with mathematical models to investigate pest suppression, the stability of pest–enemy interactions and the effects of multiple natural enemy species on suppression and stability. We use as a model system, a naturally occurring host–parasitoid community that exhibits many of the key attributes of pest–enemy systems. The framework we develop, which involves simple models parameterized with data easily obtained in laboratory experiments, serves as a guideline for assessing the suitability of natural enemy candidates as potential pest control agents.

## Materials and methods

### BIOLOGY AND NATURAL HISTORY

The harlequin bug (*Murgantia histrionica*) is a specialist herbivore on Bladderpod (*Isomeris arborea*) in the south-western United States (English 1983). The harlequin bug lacks natural predators, which is thought to be due to the sequestration of secondary compounds from the host plant (Nuss 1983). The bug's only natural enemies are the two specialist egg parasitoids (*Trissolcus murgantiae* and *Ooencyrtus johnsonii*) (Walker & Anderson 1933; Huffaker 1941). In southern California, the bug has three overlapping generations per year, and each parasitoid species has 10 generations per year (Amarasekare 2000a).

Harlequin bugs oviposit underneath *Isomeris* leaves and on pods (English 1983). Eggs are typically laid in clutches of 12, and the egg stage lasts for 15–30 days depending on the season (Amarasekare 2000a,b). *Trissolcus* is a solitary parasitoid, that is, only a single para-

sitoid larva can develop within a single host egg. *Ooencyrtus* is a gregarious parasitoid, that is, 1–3 parasitoid larvae can develop within a single host egg.

The harlequin bug and its parasitoids exhibit many attributes of pest–enemy systems in general, and of Homopteran pest systems in particular. First, the bug is a specialist herbivore on a long-lived host plant, similar to many Homopteran pests that attack long-lived crop plants (e.g. citrus, olive and stone fruits; Clausen 1978; Murdoch, Swarbrick & Briggs 2006), and its only natural enemies are the two specialist parasitoids. Second, the bug and parasitoids exhibit the same life history and population dynamics as Homopteran pest systems, with an invulnerable adult stage of the herbivore and a persistent host–parasitoid interaction with host densities maintained at low levels (Amarasekare 2000a,b, 2003). Third, the parasitoids engage in the same types of interactions as the natural enemies of Homopteran pests (exploitative competition and multiparasitism; Amarasekare 2000a,b, 2003, 2007). Fourth, the bug is a minor pest of crucifers in the south-eastern United States and the parasitoids are potential control agents (Huffaker 1941; Miller 1971). These attributes make this community an ideal model system for investigating the efficacy of natural enemies in pest suppression.

### FUNCTIONAL RESPONSES AND CONVERSION EFFICIENCIES

Our goal is to determine the degree of which each parasitoid species can suppress host abundance and its potential to maintain a stable interaction with the host. The first step therefore is to quantify the functional response and conversion efficiency of each parasitoid species.

Naive individuals of each parasitoid species were allowed to mate for 48 h with access to food (honey) and water at 24 °C. Females from these naive populations were placed individually in 2" × 2" × 4" plexiglass containers and exposed to a given egg density for 24 h at 24 °C. Female wasps were provided with water but no honey during this period. Individual females were exposed to the following range of egg densities: *Trissolcus*: 6, 12, 18, 24, 30, 36 and 39 eggs and *Ooencyrtus*: 6, 12, 18, 21, 24, 27 and 36 eggs. (*Trissolcus* was exposed to a greater range of egg densities because it was known to have a high parasitism rate even at high egg densities; Amarasekare 2007.) After 24 h, the eggs were removed and placed in labelled vials. The total number of parasitoid offspring that emerged was recorded for each egg density. Parasitized eggs were examined under a dissecting microscope to verify emergences, and unhatched eggs were dissected to determine whether unemerged parasitoid larvae were present. We conducted six replicates of the experiment for each parasitoid species.

The functional response for each egg density was quantified as the number of host eggs attacked by a single parasitoid female within 24 h. In parasitoids, attacking a host means oviposition. Host eggs from which adult parasitoids had emerged were considered as successful ovipositions, as were those eggs that failed to hatch but contained a larval parasitoid.

We quantified the risk of parasitism as the fraction of host eggs attacked by a single parasitoid female. For instance, if a female was exposed to 12 host eggs and parasitized 10 of the host eggs within 24 h, the per capita attack rate was 10 and the risk of parasitism was  $10/12 = 0.83$ . The risk of parasitism quantifies the nature of density dependence in the functional response. If the risk increases with increasing density, as it initially does in the case of a Type III functional response (Murdoch & Oaten 1975; Murdoch, Briggs & Nisbet 2003), density dependence is negative and has a stabilizing effect on host–parasitoid dynamics; if the risk decreases monotonically with

increasing density, as in the case of a Type II functional response, density dependence is positive and has a destabilizing effect on host–parasitoid dynamics (Murdoch *et al.* 2003).

We quantified the conversion efficiency of each female parasitoid as the number of parasitoid offspring emerged divided by the number of host eggs successfully attacked. For instance, if a female had attacked 10 eggs of a total of 12 host eggs offered and these 10 eggs yielded eight offspring, the conversion efficiency was  $8/10 = 0.8$ .

STATISTICAL ANALYSES

The first step in the analysis is to determine the nature of the functional response, that is whether it is linear (Type I), saturating (Type II) or sigmoid (Type III). We conducted a logistic regression analysis using a model developed by Juliano (2001):

$$\frac{E_p}{E_0} = \frac{e^{(n_0+n_1E_0+n_2E_0^2+n_3E_0^3)}}{1 + e^{(n_0+n_1E_0+n_2E_0^2+n_3E_0^3)}} \quad \text{eqn 1}$$

where  $E_p$  is the number of host eggs parasitized,  $E_0$  is the initial number of host eggs, and  $n_0, n_1, n_2$  and  $n_3$  are parameters to be estimated by the regression. A cubic model was used because it provides a good fit to a Type III functional response (Trexler, McCulloch & Travis 1988; Juliano 2001). A quadratic model is generally sufficient to detect a Type II functional response. With a Type II functional response,  $E_p/E_0$  declines monotonically with egg density whereas with a Type III functional response,  $E_p/E_0$  increases initially with egg density before starting to decline. Hence, the linear coefficient  $n_1$ , the sign of which is negative for Type II and positive for Type III, can be used to distinguish between saturating and sigmoid functional responses. A linear coefficient statistically indistinguishable from zero indicates a Type I functional response.

The second step in the analysis is to estimate the parameters of the functional response. We used both the standard functional response equations (e.g. Holling’s disc equation; Holling 1959a,b) that give instantaneous measures of the number of hosts attacked and a modified version (e.g. Rogers’s random parasitoid equation; Rogers 1972) that allows for host depletion during the experiment, that is, because there are only a fixed number of hosts present, the number of encounters with the host exceeds the number of hosts parasitized.

Holling’s disc equation for a Type II functional response is:

$$H_p = \frac{aTH}{1 + aT_hH} \quad \text{eqn 2}$$

where  $H$  is the total number of hosts available for parasitism,  $H_p$  is the number of hosts parasitized by a single parasitoid,  $T$  is the total time during which eggs were exposed to an individual parasitoid,  $a$  is the attack rate, and  $T_h$  is the handling time, that is, the time taken for an individual parasitoid to oviposit in a single host egg.

The random parasitoid equation for a Type II functional response (Rogers 1972) is derived as follows. When parasitoids search randomly for hosts, the total number of encounters between hosts and parasitoids ( $E'$ ) is given by  $E' = a''HP$  where  $a''$  is the encounter rate,  $H$  is the host abundance, and  $P$  is the parasitoid abundance. Then, the number of hosts parasitized by a single parasitoid is:

$$H_p = H\left(1 - e^{-\frac{E'}{H}}\right) = H\left(1 - e^{-a''P}\right). \quad \text{eqn 3}$$

When parasitoids search randomly, the number of encounters that a single parasitoid has with hosts ( $E$ ) is given by  $E = E'/P = a''H$ . This number is a function of the search time ( $T_s$ ) and host density ( $H$ ), that is,  $E = a'T_sH$  where  $a'$  is the search rate and  $a'T_s = a''$ . If the total time available for searching is  $T$  and  $T_h$  is the time taken for the parasitoid to handle (e.g. oviposit in) a single host,  $T_s = T - T_hE$ . Then we have,

$$E = d'(T - T_hE)H = \frac{d'TH}{1 + d'T_hH} \quad \text{eqn 4}$$

From Eqns 3 and 4,  $E'/HP = E/H = a'T/(1 + d'T_hH)$ , and we get the random parasitoid equation:

$$H_p = H\left(1 - e^{-\left(\frac{d'T}{1+d'T_hH}\right)}\right). \quad \text{eqn 5}$$

The Type III functional response with instantaneous rates (Murdoch *et al.* 2003) is given by:

$$H_p = \frac{aTH^2}{1 + aT_hH^2}, \quad \text{eqn 6}$$

and the random parasitoid equation for a Type III functional response is:

$$H_p = H\left(1 - e^{-\left(\frac{d'TH}{1+d'T_hH^2}\right)}\right). \quad \text{eqn 7}$$

The random parasitoid equation is derived under the assumption that all encounters with hosts involve a handling time  $T_h$ . In reality, only those encounters that lead to an actual attack (oviposition) involves a handling time. Hence, Rogers’s original formulation (Rogers 1972) underestimates the search time and overestimates the attack rate. In fact, the parameter  $a'$  in the random parasitoid equation is the number of hosts discovered per unit time, which includes the rediscovery of previously parasitized hosts. To estimate the real attack rate, that is, the number of hosts in which the parasitoid oviposits per unit time, one needs to distinguish between the time spent ovipositing in hosts (handling time) and the time spent examining rediscovered hosts without ovipositing. We do this with the following modification of the random parasitoid equation.

Noting that the encounter rate for a single parasitoid is  $E = a'T_sH$ , we can express the search time as  $T_s = T - T_hH_p - T_e(E - H_p)$ , that is, encounters that result in an oviposition involve a handling time  $T_h$  and encounters that do not lead to an oviposition involve a handling time  $T_e$ . Then  $E = d'H((T - H_p(T_h - T_e))/(1 + d'T_eH))$ , which leads to:

$$H_p = H\left(1 - e^{-\frac{d'(T-H_p(T_h-T_e))}{1+d'T_eH}}\right). \quad \text{eqn 8}$$

Once host depletion has been accounted for by estimating  $T_h$  and  $T_e$  separately, one can estimate the actual attack (oviposition) rate ( $a$ ) as follows. The number of hosts parasitized by an individual parasitoid  $H_p = aT_sH$  where  $T_s = (T - T_hH_p)$ . Then,  $H_p = (aTH)/(1 + aT_hH)$ . Once  $T_h$  has been estimated, fitting this equation to data allows one to estimate  $a$ .

We used nonlinear regression to fit the experimental data for each species to the appropriate functional response suggested by the logistic regression analysis. We used a two-way ANOVA with egg density and species as main effects to investigate whether there were qualitative differences between the functional responses of the two species. A statistically significant species  $\times$  egg density interaction would indicate species-specific differences in the nature of the functional response. All analyses were conducted using the SAS statistical package (SAS Institute 2003, Cary, North Carolina, USA).

POPULATION MODEL

We used a simple population model to investigate host–parasitoid dynamics and host suppression:

$$\begin{aligned} \frac{dH}{dt} &= rH \left(1 - \frac{H}{K}\right) - g_i(H, P)P_i \\ \frac{dP_i}{dt} &= e_i g_i(H, P)P_i - d_i P_i \end{aligned} \quad \text{eqn 9}$$

where  $H$  is the host density and  $P_i$  and  $g_i(H)$  are, respectively, the density and the functional response (Type II or Type III) of parasitoid species  $i$  ( $i = 1, 2$ ). The parameters  $r$  and  $K$  are, respectively, the intrinsic growth rate and carrying capacity of the host, and  $e_i$  and  $d_i$  are, respectively, the conversion efficiency and background mortality rate of parasitoid species  $i$ . We consider functional responses to be a function of both host and parasitoid density. This is because we want to investigate the effects of intraspecific interference between adult parasitoids, which can reduce their effectiveness in the field. Intraspecific interference can be incorporated into a Type II functional response as follows:  $g(H, P) = (a_i HT) / (1 + a_i T_h H + b_i P_i)$  (Beddington 1975) where  $b_i$  is the per capita strength of interference in parasitoid species  $i$ . An equivalent modification can be made to the Type III functional response as well.

We parameterized the model with the experimental data on functional responses and conversion efficiencies. We used data from other ongoing experiments (P. Amarasekare, unpublished data) on the host's intrinsic growth rate and parasitoid mortality rates. We estimated the host's carrying capacity based on field censuses of bug abundances (P. Amarasekare, unpublished data). As we do not currently have data to estimate  $b_i$ , we first analysed the model without interference and then conducted a sensitivity analysis of how variation in  $b_i$  influences host suppression and the stability of the host–parasitoid interaction. Theory predicts that intraspecific interference should decrease host suppression and increase the stability of host–parasitoid interactions in the long term (Hassell 1978, 2000; Murdoch, Chesson & Chesson 1985; Murdoch 1990, 1992; Murdoch *et al.* 1996, 2003). We investigate whether interference has different effects on the two parasitoid species' ability to suppress the host.

#### HOST SUPPRESSION AND RISK OF PARASITISM

We used the model to investigate the dynamics of the pairwise interaction between the host and each parasitoid species, and the degree of host suppression achieved by each species. We predicted the expected degree of host suppression by a given parasitoid species ( $q$ ) as  $q = (H^{*c}(\text{parasitoid})) / (H^{*c}(\text{alone}))$  where  $H^{*c}(\text{alone})$  is the equilibrium host density in the absence of the parasitoid and  $H^{*c}(\text{parasitoid})$  is the equilibrium host density in the presence of the parasitoid.

**Table 1.** Host suppression, risk of parasitism and the rate at which parasitism risk changes with host density for Type II and Type III functional responses with and without interference

Property	Functional response			
	Type II		Type III	
	No interference	Interference	No interference	Interference
Host suppression ( $q$ )	$\frac{d_i}{a_i K(e_i - a_i d_i T_{hi})}$	$\frac{eA+B}{2C} + \sqrt{\frac{d_i}{KC} + \frac{(e_i A + B)^2}{4C^2}}$ <sup>a</sup>	$\frac{\sqrt{d_i}}{K\sqrt{a_i(e_i - d_i T_{hi})}}$	— <sup>b</sup>
Parasitism risk ( $R_p$ )	$\frac{a_i T}{1 + a_i T_{hi} H}$	$\frac{a_i T}{1 + a_i T_{hi} H + b_i P_i}$	$\frac{a_i HT}{1 + a_i T_{hi} H^2}$	— <sup>b</sup>
$\frac{\partial R_p}{\partial H}$ <sup>c</sup>	$-\frac{a_i^2 T_{hi} T}{(1 + a_i T_{hi} H)^2}$	$\frac{a_i^2 T_{hi} T}{(1 + a_i T_{hi} H + b_i P_i)^2}$	$\frac{a_i T(1 - a_i T_{hi} H^2)}{(1 + a_i T_{hi} H^2)^2}$	— <sup>b</sup>

<sup>a</sup> $A = rb_i - a_i$ ,  $B = a_i d_i T_{hi}$ ,  $C = rb_i e_i$ .

<sup>b</sup>An explicit analytical expression cannot be obtained.

<sup>c</sup>The rate at which parasitism risk declines with host density.

We can also use the model to derive an analytical expression for the risk of parasitism experienced by each parasitoid species. The risk of parasitism at a given host density ( $R_p$ ) is calculated as the parasitoid species' functional response divided by the host density. The rate at which the parasitism risk declines with host density is given by  $\partial R_p / \partial H$ . Table 1 gives  $q$ ,  $R_p$  and  $\partial R_p / \partial H$  for Type II and Type III functional responses with and without interference.

## Results

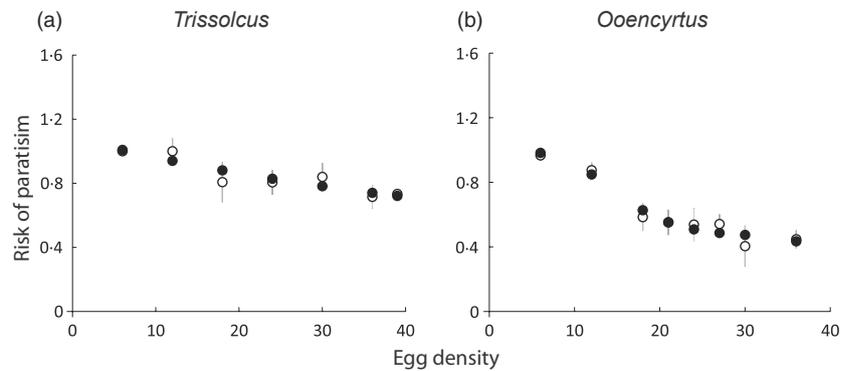
#### DETERMINING THE NATURE OF THE FUNCTIONAL RESPONSE

Logistic regression analysis using the cubic model (Eqn 1) showed that the linear coefficient was negative and significant in *Trissolcus* ( $n_1 = -0.75 \pm 0.21, P = 0.0003$ ), and negative but non-significant in *Ooencyrtus* ( $n_1 = -0.77 \pm 0.43, P = 0.15$ ). Because all coefficients were non-significant in *Ooencyrtus*, we repeated the logistic regression analysis with a simpler, quadratic model. This model yields a significant negative linear coefficient ( $n_1 = -0.3 \pm 0.08, P = 0.016$ ). These results suggest that both parasitoid species exhibit a Type II functional response. This is verified by plotting the risk of parasitism with host density, which shows that parasitism risk decreases monotonically with increasing egg density for both species (Fig. 1). The two-way ANOVA yielded a significant species  $\times$  egg density interaction ( $F = 14.1, P = 0.0037, \text{d.f.} = 1, 10$ ), suggesting that the two species exhibit qualitatively different functional responses. Indeed, *Ooencyrtus*'s functional response saturates at lower egg densities than *Trissolcus*'s (Figs 2a, b).

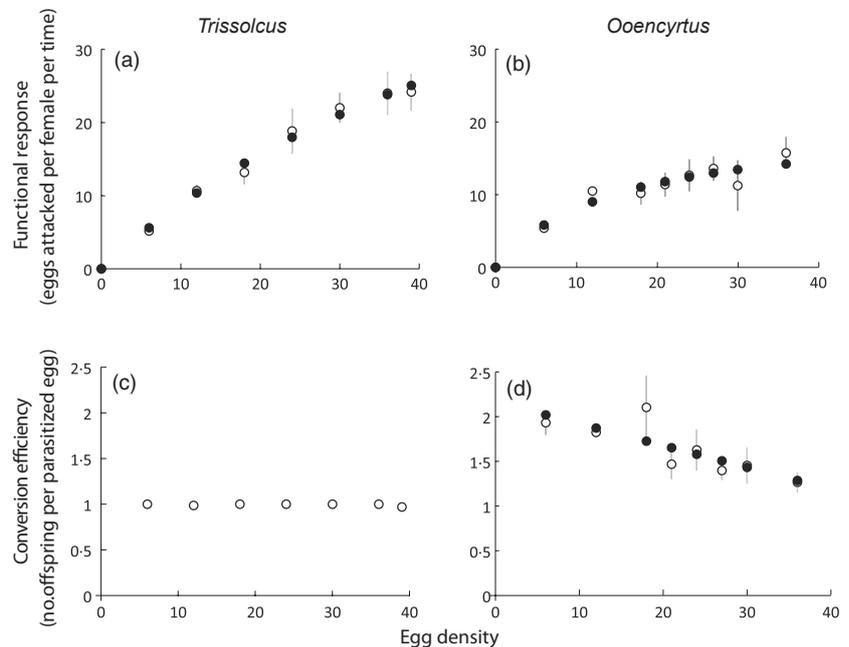
#### ESTIMATING PARAMETERS OF THE FUNCTIONAL RESPONSE

Nonlinear regression analysis was used to estimate attack rates and handling times from the observed functional response data. Table 2 provides the estimates obtained using Holling's disc equation, the random parasitoid equation and the modified random parasitoid equation. All three models yield a higher attack rate and longer handling time for *Ooencyrtus*

**Fig. 1.** The risk of parasitism exerted on the host by each parasitoid species [panel (a): *Trissolcus*, panel (b): *Ooencyrtus*] as a function of host density. The open circles are values of risk calculated from the observed functional responses, and the filled circles are those predicted based on the parameters of the logistic regression. Note that the decline in the risk of parasitism with host density is greater for *Ooencyrtus* than for *Trissolcus*.



**Fig. 2.** Functional responses and conversion efficiencies for *Trissolcus* [panels (a) and (c)] and *Ooencyrtus* (panels (b) and (d)). In panels (a) and (b), the open circles are the observed functional responses for each species, and the filled circles are the values predicted based on attack rate and handling time estimated from the modified random parasitoid equation for a Type II functional response. Panels (c) and (d) depict the conversion efficiencies of the two parasitoid species as a function of host egg density. *Trissolcus*'s conversion efficiency [panel (c)] is independent of host density, while *Ooencyrtus*'s conversion efficiency [panel (d)] declines with increasing host density. In panel (d), the filled circles are the predicted values from a linear regression of *Ooencyrtus*'s conversion efficiency on host density.



**Table 2.** Attack rates and handling times of the two parasitoid species as estimated from different models of Type II functional responses

Species	Parameter	Holling's disc equation	Random parasitoid equation	Modified random equation
<i>Trissolcus</i>	Search rate ( $a'$ ) (eggs/female/day)	–	$3.41 \pm 1.21$ ( $P = 0.03$ )	$3.41 \pm 1.21$ ( $P = 0.03$ )
	Attack rate ( $a$ ) (eggs/female/day)	$1.018 \pm 0.087$ ( $P < 0.0001$ )	–	$1.11 \pm 0.03$ ( $P < 0.0001$ )
	Encounter time ( $T_e$ ) (days)	–	–	$0.0176 \pm 0.003$ ( $P < 0.001$ )
	Handling time ( $T_h$ ) (days)	$0.015 \pm 0.003$ ( $P = 0.002$ )	$0.018 \pm 0.003$ ( $P = 0.001$ )	$0.0176 \pm 0.003$ ( $P < 0.001$ )
<i>Ooencyrtus</i>	Search rate ( $a'$ ) (eggs/female/day)	–	$5.65 \pm 5.56$ ( $P > 0.05$ )	$5.65 \pm 5.56$ ( $P > 0.05$ )
	Attack rate ( $a$ ) (eggs/female/day)	$1.37 \pm 0.35$ ( $P = 0.006$ )	–	$1.32 \pm 0.08$ ( $P < 0.0001$ )
	Encounter time ( $T_e$ ) (days)	–	–	$0.0465 \pm 0.007$ ( $P < 0.001$ )
	Handling time ( $T_h$ ) (days)	$0.05 \pm 0.008$ ( $P = 0.0004$ )	$0.046 \pm 0.007$ ( $P < 0.001$ )	$0.0465 \pm 0.007$ ( $P < 0.001$ )

than for *Trissolcus*. The longer handling time of *Ooencyrtus* causes it to have the more nonlinear functional response (Fig. 2) and a steeper decline in the risk of parasitism with host density (Fig. 1). The modified random parasitoid model allows one to compute both the search rate (which includes both discovery and rediscovery of hosts) and the actual attack (oviposition) rate. In both parasitoid species, the search rate is greater than the attack rate (Table 2). This is the result of host depletion, that is, searching results in

rediscovering already parasitized hosts leading to a fewer number of attacks per unit time.

CONVERSION EFFICIENCY

*Ooencyrtus*'s conversion efficiency (number of parasitoid offspring produced per host egg attacked) is significantly higher than *Trissolcus*'s (Fig. 2). Interestingly, *Trissolcus*'s conversion efficiency is independent of host (egg) density

**Table 3.** Pest population variability, stability and long-term pest suppression predicted under Type II and Type III responses with and without intraspecific interference

Property	Species	Model without interference	Model with interference <sup>a</sup>
Host suppression ( $q$ )	<i>Trissolcus</i>	0.0271	0.0293
	<i>Ooencyrtus</i>	0.0095	0.0102
Return time to equilibrium (days)	<i>Trissolcus</i>	110	45
	<i>Ooencyrtus</i>	739	104
Population fluctuations during transient period (CV)	Host	1.14	1.18
	<i>Trissolcus</i>	0.6	0.61
Parasitoid coexistence	Host	4.82	3.18
	<i>Ooencyrtus</i>	2.48	1.45
Time to exclusion	No	No	Yes if $b_1 < b_2$ No if $b_1 \geq b_2$
	30 days	40 days for $b_1 = b_2 = 0.1$	

<sup>a</sup>Considering interference to be low and of equal strength for both species (i.e.  $b_1 = b_2 = 0.1$ ). Higher values of  $b$  decrease host suppression (increase  $q$ ) and increase stability (decrease CV). For instance, when  $b_1 = b_2 = 1$ , return time to equilibrium decreases to 7 days for *Trissolcus* and 104 days for *Ooencyrtus*; CV of host population fluctuations decreases to 0.41 when *Trissolcus* alone attacks the host and to 1.33 when *Ooencyrtus* alone attacks the host.

(linear regression: slope =  $-0.0003$ ,  $P = 0.43$ ,  $R^2 = 0.05$ ), while *Ooencyrtus*'s conversion efficiency declines with increasing host density (linear regression: slope =  $-0.02$ ,  $P = 0.0139$ ,  $R^2 = 0.61$ ).

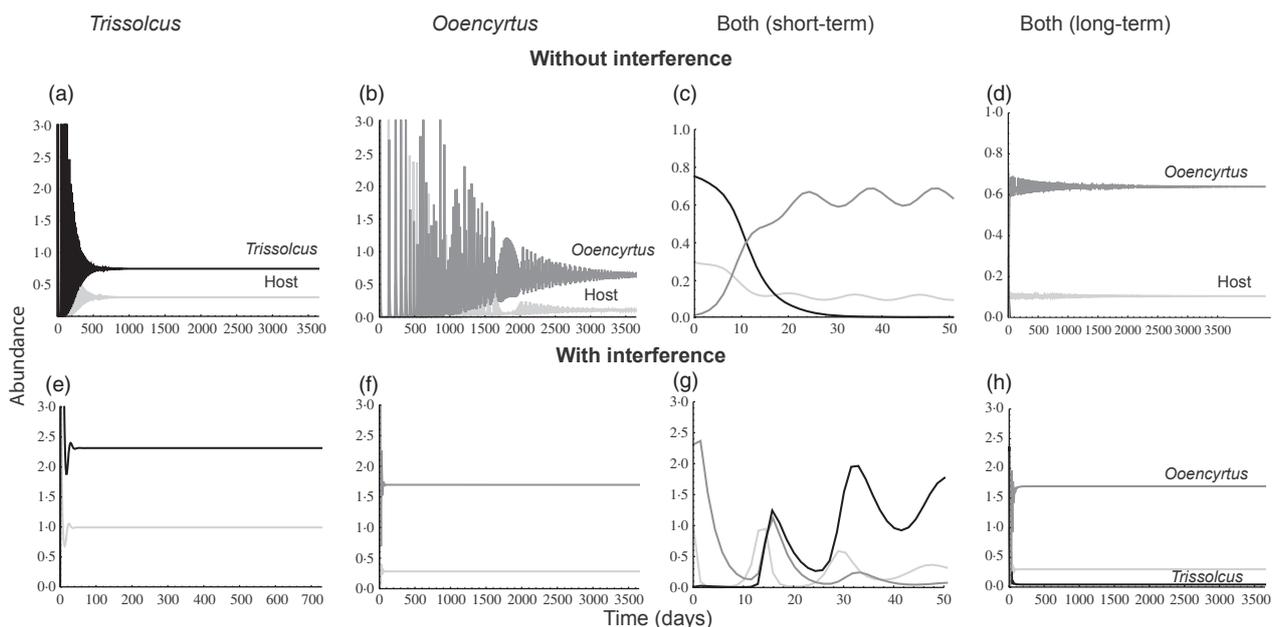
## HOST SUPPRESSION AND HOST-PARASITOID DYNAMICS

### Long-term (steady-state) outcomes

The population model (Eqn 9) parameterized with field and laboratory data predicts a stable equilibrium for both pairwise interactions (host–*Trissolcus* and host–*Ooencyrtus*) under the observed levels of host self-limitation and nonlinearity of the parasitoids' functional responses. The model also predicts high host suppression by both parasitoid species (Table 3). For instance, using attack rate and handling time estimates for the modified random parasitoid equation (Eqn 8) yields  $q = 0.0271$  for *Trissolcus* and  $q = 0.0095$  for *Ooencyrtus*. This means that both species reduce the equilibrium host abundance to  $< 1$  individual  $m^2$ . *Ooencyrtus* achieves greater pest suppression (99% reduction in the host's equilibrium abundance) than *Trissolcus* (97% reduction in the host's equilibrium abundance).

### Short-term (transient) dynamics

Although both species achieve high host suppression in the long term, they differ in the degree of host control exerted in the short term. For instance, *Ooencyrtus* takes much longer to reach its equilibrium density from initially small numbers. There is a long period of transient dynamics during which both the host and *Ooencyrtus* exhibit large fluctuations in



**Fig. 3.** Host–parasitoid dynamics predicted from the parameterized population models with and without interference. Panels (a) and (b) depict, respectively, the host–*Trissolcus* and host–*Ooencyrtus* dynamics without interference, and panels (e) and (f), the dynamics with interference ( $b_1 = b_2 = 0.1$ ). Panels (c) and (d) depict, respectively, short-term and long-term host–parasitoid dynamics when both parasitoids are initially present and there is no interference. Panels (g) and (h) depict the same dynamics with interference. In panels (c) and (g), the black line depicts *Trissolcus*'s abundance, the dark grey line depicts *Ooencyrtus*'s abundance, and the light grey line depicts the host's abundance. Excludes in the absence of interference [panels (c) and (d)], but coexistence is possible if the per capita interference strength is greater in *Ooencyrtus* [ $b_1 = 0.1$ ,  $b_2 = 1.1$  in panels (g) and (h)]. The parasitoids' attack rates, handling times and conversion efficiencies were estimated from the modified random parasitoid equation (Table 1). The other parameters, which were measured in laboratory or field experiments, are:  $r = 0.747$  per day,  $K = 11$  individuals per  $m^2$ ,  $d_1 = 0.33$  per day,  $d_2 = 0.25$ .

abundances. In contrast, *Trissolcus* reaches its equilibrium density much sooner, with a only a short period of transient fluctuations (Table 3; Fig. 3).

The length of the period of transient fluctuations can be quantified in terms of the return time to the equilibrium following a perturbation  $T_R = -1/(\text{Real}(\lambda_{max}))$ , where  $\text{Real}(\lambda_{max})$  is the real part of the largest eigenvalue of the Jacobian of Eqn 9. The return time is positive ( $T_R > 0$ ) only if the equilibrium is stable, that is, the largest eigenvalue has a negative real part. Based on parameters estimated from the modified random parasitoid equation, the return time for *Trissolcus* is 110 days (3.6 generations), while for *Ooencyrtus* it is 739 days (25 generations). Thus, there is a large difference between the two parasitoid species in their ability to return to the stable host–parasitoid equilibrium following a disturbance.

Host suppression in the short term can be quantified in terms of the host population variability during the transient period. Coefficients of variation in abundances ( $CV = S/\bar{X}$ ) calculated over the duration of transient fluctuations show that *Ooencyrtus* generates stronger host population fluctuations than *Trissolcus* (Table 3).

The reason why *Ooencyrtus* induces stronger transient fluctuations over a longer time period could be understood by comparing how host density affects the risk of parasitism experienced by an average host individual. In both parasitoid species, the risk of parasitism decreases with increasing host egg density (Fig. 1). This generates a positive density-dependent effect that causes the host to suffer overexploitation by the parasitoid when it is rare and to escape parasitoid control when it is abundant. It is this positive density-dependence that generates transient fluctuations in host and parasitoid abundance. The important point is that the higher handling time of *Ooencyrtus* causes the risk of parasitism to decline faster with host density compared to *Trissolcus* (Fig. 1). This in turn causes transient fluctuations to be stronger and longer when *Ooencyrtus* attacks the host.

#### Stability of host–parasitoid interactions

Stability of each pairwise interaction (host–*Trissolcus* and host–*Ooencyrtus*) depends on the relative strengths of host self-limitation and the degree of nonlinearity of the parasitoid's functional response. Although both parasitoid species have a stable interaction under the observed carrying capacity of the host, *Ooencyrtus*'s interaction with the host is destabilized when the host's carrying capacity is increased (Fig. 4). For instance, when the host's carrying capacity is 25% higher than that observed in the field, the interaction between the host and *Ooencyrtus* exhibits persistent fluctuations; when the carrying capacity is double that observed in the field, the interaction between the host and *Ooencyrtus* exhibits divergent fluctuations (Fig. 4). In contrast, the interaction between the host and *Trissolcus* reaches a stable equilibrium even when the host's carrying capacity is double that observed in the field (Fig. 4).

#### Interactions between parasitoid species

When both parasitoid species attack the host simultaneously, the model predicts that *Ooencyrtus* should exclude *Trissolcus* in about 30 days (Fig. 3). This is in accordance with observations in laboratory experiments, in which *Ooencyrtus* excludes *Trissolcus* within one parasitoid generation (25–30 days; P. Amarasekare, unpublished data). Competitive exclusion occurs because *Ooencyrtus*, despite having a higher handling time than *Trissolcus*, also has a higher attack rate and conversion efficiency and a lower background mortality rate. Thus, it is able to suppress the host to a lower level than *Trissolcus*. This can be seen clearly when we look at the equilibrium host abundance under each parasitoid:  $H^{*i} = d_i / (a_i(e_i - d_i T_{hi}))$ . The higher the attack rate and conversion efficiency and lower the background mortality rate of the parasitoid, the lower the equilibrium host abundance. Competitive exclusion of *Trissolcus* by *Ooencyrtus* occurs regardless of the magnitude of the host carrying capacity. For instance, even when host self-limitation is weak and *Ooencyrtus*'s interaction with the host leads to persistent fluctuations (Fig. 4), the average host abundance is not increased above the level required for *Trissolcus* to increase when rare.

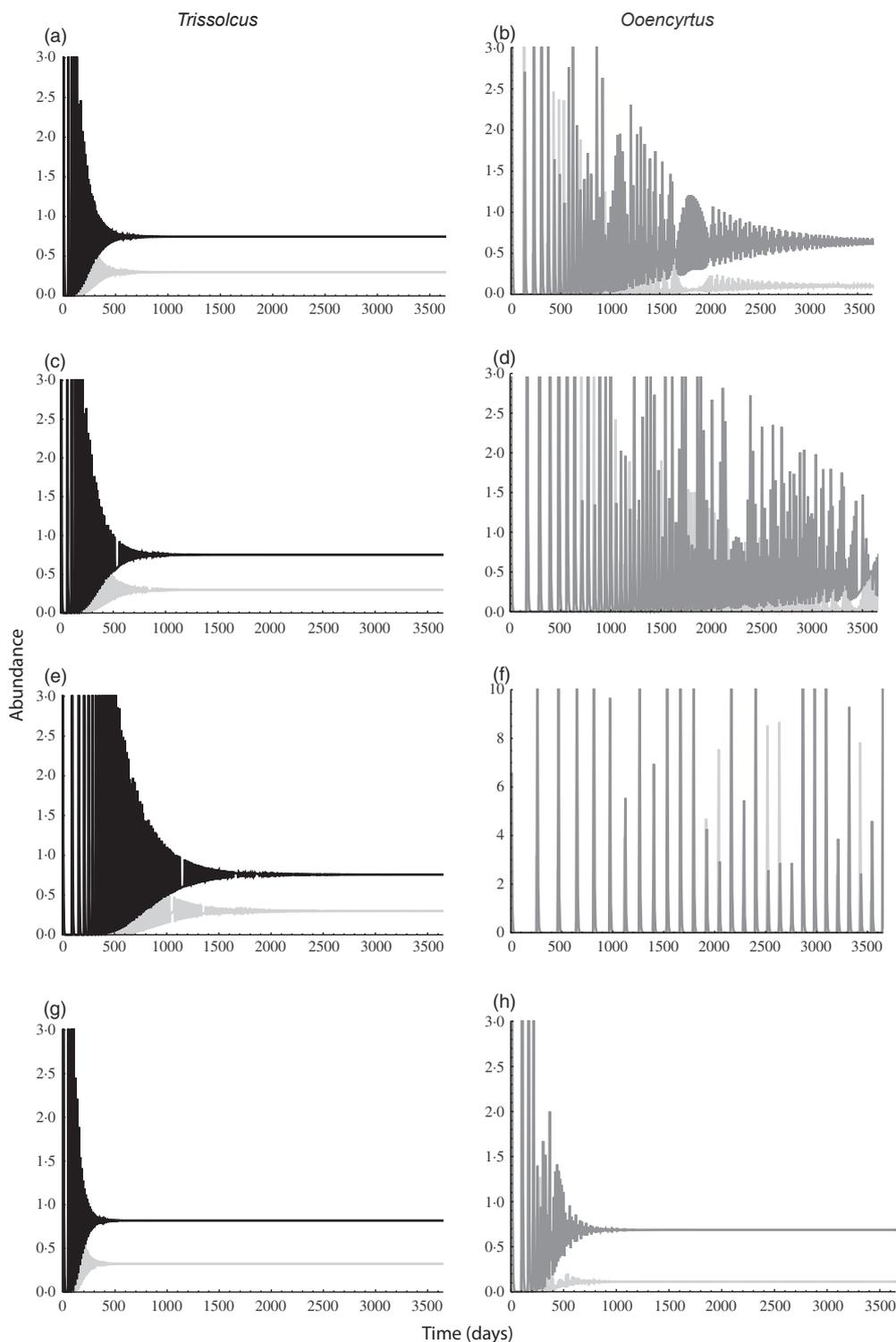
#### EFFECTS OF INTRASPECIFIC INTERFERENCE ON HOST SUPPRESSION AND HOST–PARASITOID DYNAMICS

As expected, interference decreases host suppression ( $q$ ) in the long-term (Table 3). However, it improves host control in the short-term by damping transient fluctuations in host abundance. Effects of interference on long-term host suppression is similar in both parasitoid species (i.e.  $\approx 8\%$  decline in  $q$ ). However, interference effects short-term (transient) dynamics differ radically. For instance, the decline in host population variability because of interference is effectively zero for *Trissolcus*, which induces only weak transient fluctuations in the absence of interference. In contrast, there is a 35% decline in host population variability because of the same level of interference in *Ooencyrtus*, which induces strong transient fluctuations in the absence of interference. The key point to appreciate it that even small amounts of intraspecific interference can counteract the destabilizing effect of a saturating functional response leads to a significant increase in host control in the short term with only a small decrease in host suppression in the long term.

Interference also influences interactions between parasitoid species. While the parasitoids cannot coexist in the absence of intraspecific interference, they can do so if the per capita interference strength ( $b$ ) is greater in *Ooencyrtus* than in *Trissolcus* (Table 3, Fig. 3).

#### Discussion

The ability to maintain a pest at stable, low abundances is the key criterion in selecting natural enemies as biological control agents. Although attack rates and handling times of potential control agents are routinely measured in laboratory



**Fig. 4.** Host–parasitoid dynamics when the host’s carrying capacity is increased above that observed in the field. Panels (a) and (b) depict the dynamics under the observed host carrying capacity for *Trissolcus* and *Ooencyrtus*, respectively. Panels (c) and (d) depict the dynamics when the host’s carrying capacity is 25% higher than that observed in the field. Panels (e) and (f) depict the dynamics when the host’s carrying capacity is double that observed in the field. Panels (g) and (h) depict the increase in stability because of intraspecific interference when the host’s carrying capacity is doubled.

experiments (e.g., Cave & Gaylor 1989; Bezemer & Mills 2001; Gitonga *et al.* 2002; Fernandez-arhex & Corley 2003; Lee & Kang 2004; Rutledge & O’Neill 2005; Seko & Miura 2008; Britto *et al.* 2009), it is rarely that these data are

combined with population models to predict the degree of pest suppression likely to be achieved by a given control agent. When multiple natural enemy species are being considered as control agents, models parameterized with data can

also predict the outcome of interactions between enemy species (coexistence vs. exclusion) and whether pest suppression is likely to be greater with multiple enemies. Such information is crucial in developing scientifically sound biological control strategies that are also cost-effective.

Here, we use a combination of laboratory experiments and mathematical models to investigate pest suppression and the stability of pest–enemy interactions. We use as a model system a host–parasitoid community that exhibits many key features of pest–enemy systems. We report three key findings.

First, the interplay between the host's self-limitation and the parasitoids' saturating functional response causes the long-term (steady-state) outcomes for host suppression to differ from the outcomes of short-term (transient) dynamics. For instance, when the host's self-limitation is moderately strong, as appears to be the case with the harlequin bug, the parasitoid species with the higher attack rate and conversion efficiency (*Ooencyrtus*) achieves greater host suppression in the long term, but its higher handling time causes long periods of transient dynamics during which the host can reach high abundances. When the host's self-limitation is weak, *Ooencyrtus*'s longer handling time induces host fluctuations of increasing magnitude, causing it to fail at host suppression both in the short term and the long term. In contrast, the parasitoid species with the lower attack rate and conversion efficiency but the shorter handling time (*Trissolcus*) induces only weak transient fluctuations of short duration and can maintain the host at stable, low abundances regardless of the strength of the host's self-limitation.

The difference between the two parasitoid species in their effects on short-term (transient) dynamics arises from the differential risk of parasitism they impose on the host. Because both species exhibit saturating (Type II) functional responses, the risk of parasitism experienced by an average host individual decreases with increasing host density (Fig. 1). However, because *Trissolcus* has a lower handling time than *Ooencyrtus*, the decline in the risk of parasitism with host density is much less steep for *Trissolcus* than for *Ooencyrtus*. Thus, *Trissolcus* has less of a tendency than *Ooencyrtus* to overexploit the host at low host densities and to underexploit the host at high host densities. Thus, population fluctuations resulting from alternative periods of host escape and parasitoid overexploitation are less likely when *Trissolcus* alone attacks the host.

These results highlight the importance of transient dynamics in pest suppression by natural enemies. Most theory on pest–enemy interactions focuses on long-term, steady-state outcomes for pest suppression (Hassell 1978, 2000; Murdoch *et al.* 1985; Ehler 1990; Waage 1990; Murdoch 1990, 1992; Waage & Mills 1992; Murdoch *et al.* 1996, 2003; Murdoch & Briggs 1996). However, pest–enemy interactions, and all consumer–resource interactions in general, are characterized by short-term fluctuations in abundance that either persist, decay or amplify depending on the strength of pest self-limitation relative to the natural enemy's effect (via its functional and numerical responses) on the pest. Pest species are unlikely to be strongly self-limited, given that they attack

monocultures of crops that present little or no resource limitation. Hence, fluctuations in pest and enemy abundance are likely to dominate short-term dynamics even when the long-term outcome is a stable equilibrium. Furthermore, pest–enemy communities, particularly those inhabiting annual crops, are subject to frequent disturbances, such as tilling and harvesting. Such disturbances will intensify the tendency for transient fluctuations and prevent pests and enemies from attaining stable equilibria. For instance, an enemy species with a high attack rate and conversion efficiency but a long handling time will have a longer return time to equilibrium following a perturbation, during which the pest and enemy abundances will fluctuate and the pest can reach outbreak levels. If disturbances are frequent, transient dynamics will dominate and the enemy will be ineffective at pest suppression. An enemy species with a shorter handling time, even if it has a lower attack rate and/or conversion efficiency, is likely to provide more effective control because it will have a faster return time to equilibrium and hence a shorter period of transient fluctuations that are also weaker in amplitude.

Our second major finding concerns the use of multiple natural enemies in pest control. Simultaneous release of multiple natural enemies can compromise pest suppression if an enemy species that induces greater transient fluctuations in the pest excludes an enemy that induces weaker fluctuations. For instance, in laboratory experiments when both parasitoids are initially present, *Ooencyrtus* excludes *Trissolcus* despite having a longer handling time because it has a higher conversion efficiency. A host–multiparasitoid model parameterized with data correctly predicts the time to exclusion observed in experiments, suggesting that the modelling framework we have used is able to capture the essential biological features of host–parasitoid (and by extension, pest–enemy) interactions.

Our third major finding pertains to the role of intra-specific interference in influencing pest suppression and pest–enemy dynamics. Classical host–parasitoid theory predicts that intra-specific interference should be detrimental to biological control because it reduces pest suppression in the long term (e.g. Murdoch 1990, 1992; Murdoch *et al.* 1996, 2003). This body of theory, however, has not considered the impact of transient dynamics on pest suppression. Our approach of investigating both short-term (transient) dynamics and long-term (steady-state) outcomes yields new insights into the role of intraspecific interference in pest suppression. Specifically, we find that interference reduces long term pest suppression but improves pest control in the short term by reducing the magnitude and duration of transient fluctuations in pest abundance. If the strength of intra-specific interference is not so strong as to severely reduce pest control in the long-term, enemy species that engage in interference may be preferable to species that do not, especially in the case of species like *Ooencyrtus* that combines desirable properties such as high conversion efficiency and low mortality with undesirable ones such as a long handling time.

As we have shown here, integrating laboratory experiments with dynamical models leads to novel insights about

biological pest control that could not have been elucidated based on experiments alone or based on theory that focuses only on long-term (equilibrium) outcomes. The most crucial insight to emerge is the role of transient dynamics in pest suppression. By focusing on both short-term dynamics and long-term outcomes, we have found that natural enemy traits that reduce large fluctuations in pest abundance in the short term (e.g. short handling times) are as important as traits that ensure pest suppression in the long term (e.g. high attack rates and conversion efficiencies). The ideal trait combination for pest suppression in both the short term and the long term is a high attack rate and conversion efficiency and a short handling time. However, most natural enemy species in nature are constrained by life history and energetic trade-offs that cause them to deviate from the ideal trait combination. For instance, parasitoids with high conversion efficiency typically have longer handling times because females deposit multiple eggs within a single host; parasitoids with high searching ability because they are strong fliers tend to have low conversion efficiency because their body size constrains the number of offspring that can develop within a single host. These biological realities make it crucial that experiments on functional responses be combined with dynamical models of pest–enemy interactions so that the ability of a potential control agent to achieve both short-term and long-term control can be predicted in advance. The mathematical analyses we have used here provide a useful set of guidelines for choosing appropriate control agents for a given pest.

Recent years have seen an increase in the awareness of the importance of transient dynamics in both basic and applied ecology (e.g. Fox & Gurevitch 2000; Hastings 2004, 2010; Yearsley 2004; Caswell & Neubert 2005; Caswell 2007; Haridas & Tuljapurkar 2007; Ezard *et al.* 2010). More than a few studies have shown that natural or anthropogenic perturbations can have differential effects on vital rates and age/structure of populations, leading to short-term dynamics that are markedly different from the expected asymptotic outcomes (e.g. Koons, Grand & Arnold 2006; Koons *et al.* 2007; Ezard *et al.* 2010). Such discrepancies have been observed in invasive plant species (Mertens, Yearsley, den Bosch & Gilligan 2006; Ezard *et al.* 2010), birds and mammals (Koons *et al.* 2005, 2006; Ozgul *et al.* 2009), and populations subjected to harvesting (Solberg, Saether, Strand & Loison 1999). While there has been a great deal of work on the importance of transient dynamics in conservation and resource management, no studies to date have examined their role in biological pest control. Our work provides a starting point for further investigations of the role of transient population phenomena in pest–enemy interactions.

A common criticism of simple dynamical models, such as the ones used here, is that they do not capture the spatial and temporal heterogeneities inherent in natural systems. The fact that the model, when parameterized with data for the host–parasitoid community, correctly predicts key attributes such as the time to exclusion is encouraging because it suggests that the model contains sufficient biological complexity to capture the essential features of pest–enemy interactions.

Moreover, simple models are particularly appropriate in biological control because agricultural communities lack much of the spatial complexities observed in natural communities. Temporal variation, on the other hand, is likely to be as important in agricultural systems as it is in natural systems. If pest species inhabit seasonal environments and potential control agents exhibit differential responses to seasonal variation, a simple extension of the models analysed here could address the issue of how temporal variation in key parameters influences pest suppression and pest–enemy dynamics.

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## References

- Amarasekare, P. (2000a) Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. *Ecology*, **81**, 1286–1296.
- Amarasekare, P. (2000b) Spatial dynamics in a host–multiparasitoid community. *Journal of Animal Ecology*, **69**, 201–213.
- Amarasekare, P. (2003) Diversity–stability relationships in multi-trophic systems: an empirical exploration. *Journal of Animal Ecology*, **72**, 713–724.
- Amarasekare, P. (2007) Trade-offs, temporal variation and species coexistence in communities with intraguild predation. *Ecology*, **88**, 2720–2728.
- Beddington, J.R. (1975) Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology*, **44**, 331–340.
- Bezemer, T.M. & Mills, N.J. (2001) Host density responses of *Mastrus ridibundus*, a parasitoid of the codling moth, *Cydia pomonella*. *Biological Control*, **22**, 169–175.
- Bierzychudek, P. (1999) Looking backwards: assessing the projections of a transition matrix model. *Ecological Applications*, **9**, 1278–1287.
- Britto, E.P.J., Gondim, M.C.G.Jr, Torres, J.B, Fiabo, K.K.M., Moreas, G.J., Knapp, M. (2009) Predation and reproductive output of the ladybird beetle *Stethorus tridens* preying on tomato red spider mite *Tetranychus evansi*. *Bio-Control*, **54**, 363–368.
- Caswell, H. (2007) Sensitivity analysis of transient population dynamics. *Ecology Letters*, **10**, 1–15.
- Caswell, H. & Neubert, M. (2005) Reactivity and transient dynamics of discrete-time ecological systems. *Journal of Difference Equations and Applications*, **11**, 295–310.
- Cave R.D. & Gaylor, M.J. (1989) Functional response of *Telonomus reynoldsi* (Hym.: Scelionidae) at five constant temperatures and in an artificial plant arena. *Entomophaga*, **34**, 3–10.
- Clausen C.P. (1978) *Introduced Parasites and Predators of Arthropod Pests and Weeds: A World Review*. Agricultural handbook no. 480, Agricultural Research Service, USDA, Washington, DC.
- Clutton-Brock, T. & Coulson, T. (2002) Comparative ungulate dynamics: the devil is in the detail. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences*, **357**, 1285–1298.
- Coulson, T., Guinness, F., Pemberton, J. & Clutton-Brock, T. (2004) The demographic consequences of releasing a population of red deer from culling. *Ecology*, **85**, 411–422.
- Dixon, A.F.G. (2000) *Insect Predator-prey Dynamics: Ladybird Beetles and Biological Control*, 257 pp. Cambridge University Press, UK
- Ehler, L.E. (1990) Introduction strategies in biological control of insects. *Critical Issues in Biological Control* (eds M. Mackauer, L.E. Ehler & J. Roland), pp. 111–134. Andover Press, UK.
- English, K.J. (1983) *Development and mortality of Murgantia histrionica in relation to food quality*. MS thesis, San Diego State University, San Diego.
- Ezard, T.H.G., Bullock, J.M., Dalglish, H.M., Millon, A., Pelletier, F., Ozgul, A. & Koons, D.N. (2010) Matrix models for a changeable world: the importance of transient dynamics in population management. *Journal of Applied Ecology*, **47**, 515–523.

- Fernandez-arhex V. & Corley, J.C. (2003) The Functional Response of Parasitoids and its Implications for Biological Control. *Biocontrol Science and Technology*, **13**, 403–413.
- Fox, G.A. & Gurevitch J. (2000) Population numbers count: tools for near-term demographic analysis. *American Naturalist*, **156**, 242–256.
- Gitonga, L.M., Overholt, W.A., Loohr, B., Magambo, J.K. & Muekec, J.M. (2002) Functional response of *Orius albidipennis* (Hemiptera: Anthocoridae) to *Megalurothrips sjostedti* (Thysanoptera: Thripidae). *Biological Control*, **24**, 1–6.
- Godfray, H.C.J. & Waage, J. (1991) Predictive modelling in biological control: the mango mealy bug (*Rastrococcus invadens*) and its parasitoids. *Journal of Applied Ecology*, **28**, 434–453.
- Haridas, C.V. & Tuljapurkar, S. (2007) Time, transients and elasticity. *Ecology Letters*, **10**, 1143–1153.
- Hassell M.P. (1978) *The Dynamics of Arthropod Predator-prey Systems*. Princeton University Press, Princeton, NJ.
- Hassell M.P. (2000) *The Spatial and Temporal Dynamics of Host-parasitoid Interactions*. Oxford University Press, Oxford.
- Hastings A. (2004) Transients: the key to long-term ecological understanding? *Trends in Ecology and Evolution*, **19**, 39–45.
- Hastings A. (2010) Time scales, dynamics and ecological understanding. *Ecology*, **91**, 3471–3480.
- Holling, C.S. (1959a) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist*, **91**, 293–320.
- Holling, C.S. (1959b) Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, **91**, 385–398.
- Huffaker C.B. (1941) Egg parasites of the harlequin bug in North Carolina. *Journal of Economic Entomology*, **34**, 117–118.
- Juliano, S. (2001) Non-linear curve fitting: predation and functional response curves. *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch), pp. 159–182. Chapman and Hall, New York.
- Koons, D.N., Grand, J.B., Zinner, B. & Rockwell, R.F. (2005) Transient population dynamics: relations to life history and initial population state. *Ecological Modelling*, **185**, 283–297.
- Koons, D.N., Grand, J.B. & Arnold, J.M. (2006) Population momentum across vertebrate life histories. *Ecological Modelling*, **197**, 418–430.
- Koons, D.N., Holmes, R.R. & Grand, J.B. (2007) Population inertia and its sensitivity to changes in vital rates and population structure. *Ecology*, **88**, 2857–2867.
- Lee, J. & Kang, T. (2004) Functional response of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) to *Aphis gossypii* Glover (Homoptera: Aphididae) in the laboratory. *Biological Control*, **31**, 306–310.
- Mertens, S.K., Yearsley, J.M., den Bosch, F. & Gilligan, C.A. (2006) Transient population dynamics in periodic matrix models: methodology and effects of cyclic permutations. *Ecology*, **87**, 2238–2348.
- Miller, M. (1971) Regulation of populations of the harlequin bug, *Murgantia histrionica* by egg parasites. *Journal of Georgia Entomological Society*, **6**, 254–257.
- Murdoch, W.W. (1990) The relevance of pest-enemy models for biological control. *Critical Issues in Biological Control* (eds M. Mackauer, L.E. Ehler & J. Roland), pp. 1–24. Andover Press, U.K.
- Murdoch, W.W. (1992) Ecological theory and biological control. *Applied Population Biology* (eds S.K. Jain & L.W. Botsford), pp. 197–221. Springer, Netherlands.
- Murdoch W.W. & Briggs, C.J. (1996) Theory for biological control: recent advances. *Ecology*, **77**, 2001–2013.
- Murdoch W.W. & Oaten, A. (1975) Predation and population stability. *Advances in Ecological Research*, **9**, 1–131.
- Murdoch, W.W., Chesson, J. & Chesson, P.L. (1985) Biological control in theory and practice. *American Naturalist*, **125**, 344–366.
- Murdoch, W.W., Briggs, C.J. & Nisbet, R.M. 1996. Competitive displacement and biological control in parasitoids: a model. *American Naturalist*, **148**, 807–826.
- Murdoch, W.W., Briggs C.J. & Nisbet, R.M. (2003) *Consumer-resource Dynamics*. Princeton University Press, Princeton NJ.
- Murdoch W.W., Swarbrick S. & Briggs C.J. (2006) Biological control: lessons from a study of California red scale. *Population Ecology*, **48**, 297–305.
- Nuss, C. (1983) *Feeding behavior and within-host feeding preferences of the harlequin bug, Murgantia histrionica, on the bladderpod plant, Isomeris arboorea*. MS Thesis, San Diego State University, San Diego.
- Ozgul, A., Oli, M.K., Armitage, K.B., Blumstein, D.T. & van Vuren, D.H. (2009) Influence of local demography on asymptotic and transient dynamics of a yellow-bellied marmot metapopulation. *American Naturalist*, **173**, 517–530.
- Rogers, D. (1972) Random search and insect population models. *Journal of Animal Ecology*, **41**, 369–383.
- Rutledge, C.E. & O'Neill, R. 2005. *Orius insidiosus* (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumura. *Biological Control*, **33**, 56–64.
- Seko, T. & Miura, K. (2008) Functional response of the lady beetle *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) on the aphid *Myzus persicae* (Homoptera: Aphididae). *Applied Entomology and Zoology*, **43**, 341–345.
- Solberg, E.J., Saether, B.E., Strand, O. & Loison, A. (1999) Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology*, **68**, 186–204.
- Tenhumberg, B., Tyre, A.J. & Rebarber, R. (2009) Model complexity affects transient population dynamics following a dispersal event: a case study with pea aphids. *Ecology*, **90**, 1878–1890.
- Trexler, J.C., McCulloch, C.E. & Travis, J. (1988) How can the functional response best be determined? *Oecologia*, **76**, 206–214.
- Waage, J.K. (1990) Ecological theory and the selection of biological control agents. In M. Mackauer, L.E. Ehler & J. Roland (eds.), pp. 135–157. Critical Issues in Biological control, Andover, UK.
- Waage J.K. & Mills, N.J. (1992) Biological control. *Natural Enemies: The Population Biology of Predators, Parasites and Diseases* (ed M.J. Crawley), pp. 412–430. Blackwell, Oxford.
- Walker H.G. & Anderson, L.D. (1933) Report on the control of the harlequin bug, *Murgantia histrionica* Hahn, with notes on the severity of an outbreak of this insect in 1932. *Journal of Economic Entomology*, **26**, 129–135.
- Yearsley, J.M. (2004) Transient population dynamics and short-term sensitivity analysis of matrix population models. *Ecological Modelling*, **177**, 245–258.

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