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Coexistence of attack-limited parasitoids sequentially exploiting the same resource and its implications for biological control

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Theory predicts that competing species cannot coexist on a single, non-replaceable resource unless the resource is partitioned. Host–parasitoid complexes (common in nature) admit hosts supporting more than one parasitoid species, a significant fraction of which specialize on that host. A simple one-host, two-parasitoid (1H2P) model indicates that stable three-species coexistence occurs under a wide range of conditions; shows that a parasitoid with attack aggregation sufficient to stabilize a one-parasitoid system can stabilize an otherwise-unstable two-parasitoid system; and contradicts, under these conditions, the generalization that the stronger competitor will draw down the resource to the point of excluding the weaker. When both parasitoid species are ecologically identical, except that one parasitoid species attacks earlier than the second, this difference alone is insufficient to cause competitive exclusion of the inferior competitor (the later attacker), under a wide range of host ecological values. For biological control purposes, our analysis illustrates potential conflict between the properties of a 1H2P system that provide the maximal *absolute* host suppression, and those properties that provide the maximal *additional* host suppression resulting from the presence of the second parasitoid.

Introduction

A substantial body of ecological theory suggests that competing species cannot coexist on a single, non-replaceable resource unless the resource is partitioned in some way (Grinnell 1904, Volterra 1928, Lotka 1932, Hardin 1960, Tilman 1982, 1990, Holt *et al*. 1994, Bonsall *et al*. 2002). One might thus expect that consumers competing for the same resource are either polyphagous, or that they have evolved strategies to reduce competition through resource partitioning. Parasitic wasps, however, are often host specific, and their hosts are attacked by multiple parasitoid species (Zwölfer 1971, Hochberg & Hawkins 1994). The mechanisms that maintain multiparasitoid complexes on particular host species are not well understood, although such

understanding is motivated by issues relating to the biological control of insect pests (Hassell 1978, May & Hassell 1988, Godfray 1994, Mills & Getz 1996, Murdoch & Briggs 1996, Briggs *et al*. 1999, Mills 2000), and by similarities to communities of helminth parasites (Sousa 1994).

A long-standing debate concerns the potential benefits or liabilities of introducing multiple enemies in biological control introductions (Smith 1929, Thompson 1939, van den Bosch 1968, Hassell & Varley 1969, Huffaker *et al*. 1971, Hassell 1978, May & Hassell 1981, 1988, Münster-Swendsen 1982, Waage & Hassell 1982, Hogarth & Diamond 1984). As with plants competing for a single limiting resource (Tilman 1982, 1990), theory suggests that a competitively superior parasitoid — the one that can survive on the least amount of the resource — will displace all other competitors (but *see* Getz & Schreiber 1999).

Alternatively, researchers arguing against multiple enemy introductions have pointed out, with the support of field data, that such introductions often result in higher pest densities and less effective pest control than can be obtained by the best enemy species alone (Pemberton & Willard 1918, Utida 1953, Turnbull & Chant 1961, Zwölfer 1963, Watt 1965, Godfray & Waage 1991, Briggs 1993, Briggs *et al*. 1993). They have emphasized the need to evaluate, prior to release, the efficacy of each individual enemy, and to subsequently release only the most effective one. Furthermore, as Ehler and Hall (1982) have noted, sequential multiple introductions can result in species which are introduced later being unable to establish themselves due to reduced availability of pests. This may result in inferior pest suppression if those species introduced later would otherwise have provided better control. Because it has become clear that the consequences of multiple introduction are highly situation- and biology-specific (e.g. Kakehashi *et al*. 1984), studies have been undertaken to assess ecological factors affecting parasitoid coexistence, including spatial patterns (Münster-Swendsen 1982, Hassell *et al*. 1994), degree of parasitoid specialization (Hassell & May 1986, Wilson *et al*. 1996), and ability to invade an established host–parasitoid interaction (Armstrong & McGehee 1980, Crawley 1986, Gutierrez *et al*. 1993; *see* Barlow & Wratten 1996, Mills & Getz 1996, Murdoch & Briggs 1996, Briggs *et al*. 1999, Hochberg & Holt 1999, Tuda & Bonsall 1999, and Hassell 2000a, 2000b for reviews of host–parasitoid models).

Many factors affect the attack rate of parasitoids (Sait *et al*. 1997), but it is difficult to explicitly incorporate all of these into simple models. The effects of spatial and temporal aggregating factors, such as refugia, can be incorporated implicitly without making models overly complex (e.g. May & Hassell 1981, Briggs *et al*. 1993, Rohani *et al*. 1994). Here, for the first time, we explicitly (rather than implicitly) analyze the effects of handling time and egg/fecundity limitation (Mills & Getz 1996; *see* Lane *et al*. 1999 for the definition of fecundity limitation) on parasitoids competing for the same host. The importance of egg limitation in the context of simple host–parasitoid models is often ignored (but *see* Getz & Mills 1996, Shea *et al*. 1996, Lane *et al*. 1999), although studies using more complex models have considered its effects (Griffiths & Holling 1969, Münster-Swendsen & Nachman 1978, Yamamura & Yano 1988, Kidd & Jervis 1989, Shea *et al*. 1996), doubtless due to the empirically demonstrated importance of egg and/or fecundity limitation to parasitoid behavioral ecology (Heimpel *et al*. 1996, 1998, Van Alebeek *et al*. 1996, Heimpel & Rosenheim 1998, Rosenheim 1999). Furthermore, it has been shown that parasitoid fecundity can be a significant determinant of the success or failure of biological control (Stiling 1990). Thus, a stronger theoretical understanding of the effect of fecundity limitation on host–parasitoid population dynamics, as obtained here from an analysis of an elaborated version of a discrete time two-parasitoid–one-host model first considered by May and Hassell (1981), enhances our understanding of basic consumer–resource dynamics, as well as improves our chances of successfully implementing multiple-parasitoid biological control.

The model

Our model is essentially an implementation of that of May and Hassell (1981) for the case where the parasitoids have Holling Type II func-

tional responses. Specifically, if N_t denotes the host density, P_t and Q_t the density of parasitoid females of two distinct populations, at time t, $\varepsilon_{P,t} = \varepsilon(N_t,P_t)$ and $\varepsilon_{P,t} = \varepsilon(N_t,Q_t)$ the encounter rate functions (cf. Mills & Getz 1996), $f_P = f_P(\varepsilon_{P,t})$ and $f_Q = f_Q(\varepsilon_{Q,t})$ the escape functions (representing the proportion of hosts escaping attack by the parasitoid populations P and Q, respectively), and $g(N_t)$ the host *per-capita* growth rate function, then this model has the form

$$\begin{aligned} N_{t+1} &= N_t g(N_t) f_P(\varepsilon_{P,t}) f_Q(\varepsilon_{Q,t}) \\ P_{t+1} &= c_P N_t [1 - f_P(\varepsilon_{P,t})] \\ Q_{t+1} &= c_Q N_t f_P(\varepsilon_{P,t}) [1 - f_Q(\varepsilon_{Q,t})], \end{aligned} \quad (1)$$

where the constants c_P and c_Q are defined as the average number of adult female parasitoids of populations P and Q respectively that emerge from an attacked host. The more complicated case where c_P and c_Q are influenced by population density (Hassell *et al.* 1983, Comins & Wellings 1985), which in turn influences ecological stability and parasitoid competitive ability (Kaitala & Getz 1992), and even the evolution of parasitoid virulence (Tuda & Bonsall 1999), is a topic for future investigations.

Our analysis focuses on the following special cases: density independent (DI) host population growth:

$$g(N) = \lambda \quad (\lambda > 1) \quad (2)$$

or density dependent (DD) Ricker host population growth:

$$g(N) = \exp\left[r\left(1 - \frac{N}{K}\right)\right] \quad (r > 0, K > 0) \quad (3)$$

as a function of host density N, with $r = \ln\lambda$ and carrying capacity K such that $g(K) \equiv 1$ (*see* Bellows 1981, Getz 1996, and Lane & Mills 2003 for discussion of these and other forms); negative binomial escape (mean encounter rate ε_t and aggregation parameter $k > 0$ — *see* May 1978):

$$f_P(\varepsilon_{P,t}) = \left(1 + \frac{\varepsilon_{P,t}}{k_P}\right)^{-k_P}$$

and (4)

$$f_Q(\varepsilon_{Q,t}) = \left(1 + \frac{\varepsilon_{Q,t}}{k_Q}\right)^{-k_Q};$$

and Holling Type II encounter rate functions (Holling 1959, Getz & Mills 1996, Mills & Getz 1996, Lane *et al.* 1999) (maximum encounter rate parameters a_P and a_Q, and egg-limitation parameters β_P and β_Q)

$$\varepsilon_P = \frac{a_P \beta_P P}{\beta_P + a_P N} \text{ and } \varepsilon_Q = \frac{a_Q \beta_Q Q}{\beta_Q + a_Q N}. \quad (5)$$

The structural constraint in the model (Eq. 1) that either parasitoid P attacks first, or, equivalently, that P always wins when a host is parasitized by both P and Q, can be relaxed under the assumption that the "first attacker wins" (Kakehashi *et al.* 1984, Schreiber *et al.* 2000). In such a model, however, the relative advantage of being the first to attack cannot be evaluated, as is done here. Thus, the difference in parasitoid strategies (described below) may be purely the difference in the timing of attack during the host's life-cycle, or could include differences in attack efficiency and/or lifetime fecundity.

This model can be analyzed both for the stability properties of the coexistence equilibria, and for the ability of one parasitoid to invade a persistent interaction of the other parasitoid with its host (this latter interaction could be stable or oscillatory). Our extensive numerical simulations revealed parameter values supporting three-species coexistence always corresponded to the ability of each parasitoid to invade when the other was present — this fact should be kept in mind when interpreting our results. Despite the relative simplicity of this model, the forms of the functions f and ε prevent obtaining closed-form expressions for the host and parasitoid equilibrium densities (Lane 2002). Thus, stability and host-suppression results were obtained numerically, using a simulation approach nearly identical to that employed by Hochberg and Holt (1995) to analyze two-dimensional systems (Lane 2002). In our simulations, the affects of the following combinations of parameter values were explored: λ = 1.1 or 2.0; a_R = 0.01 or 0.1; β_R = 50 or 200; k_R = 0.25 or 0.75; k_I = 0.25, 0.75 or 2.0. The subscript R refers to the resident parasitoid, in stable equilibrium with the host at the start of the simulation, and the subscript I to the invading parasitoid — we considered both

cases where the invader attacked either before or after the resident in the host's life-cycle. We fixed $c_P = c_Q = 0.2$ in all simulations, and for the DD scenarios set $K = 1000.0$, except for one case noted in the text where $K = 80.0$.

Results

The density-independent (DI) model (Eqs. 1, 2, 4 and 5) has essentially 8 free parameters: we scaled time using c_P leaving λ, a_P, β_P, k_P, a_Q, β_Q, c_Q and k_Q to take on values scaled by c_P. In the density-dependent model (Eqs. 1, 3, 4 and 5), we have an additional carrying capacity parameter K, assuming the same value applies to both parasitoids. After extensive simulations we found, for selected values of λ, k_P, c_Q and k_Q, that three-species coexistence conditions (which in our case also implies conditions for invasion of a parasitoid into an extant host–parasitoid interaction) depend strongly on the ratios of the two parasitoid fecundity parameters (β_P/β_Q) and search parameters (a_P/a_Q) rather than the absolute values of these four parameters. Thus we present stability results for both the DI and DD models by mapping out regions in ratio parameter space (horizontal axis $a_P/a_Q \geq 0$; vertical axis $\beta_P/\beta_Q \geq 0$) where the coexistence equilibrium is stable, oscillatory, or not supported (i.e. one of the parasitoid species is excluded or, equivalently, cannot invade) for different scenario values of the parameters λ, k_P, k_Q and K (Figs. 1–4). The basic stability results are illustrated in Fig. 1 while variations on the theme laid out in Fig. 1 are illustrated in Figs. 2–4.

Search efficiency and fecundity: the basic result

For each simulation one of five outcomes is possible: the host can coexist with P in the absence of Q (unshaded region closest to the origin in Figs. 1–3; unshaded region furthest from the origin in Fig. 4); the host can coexist with Q in the absence of P (unshaded region furthest from the origin in Figs. 1–3; unshaded region closest to the origin in Fig. 4); the host can coexist with both P and Q, with all three species at mathematically stable equilibrium densities (light shading in Figs. 1–4); the host can coexist with both P and Q with all three species experiencing bounded but varying densities through time (mathematically unstable equilibria or oscillatory coexistence, dark shading in Figs. 1–4); and finally the host population can grow unbounded with either or both of the parasitoid populations going extinct, or growing without bound but at a slower rate than the host population (black shading in Figs. 1–4). This last outcome is possible only when the host is not self-limiting–host density-dependence is thus always a stabilizing feature of the model, as is expected and intended. Note that regions exist (near the origin and as the values on both axes go to infinity) where one-host, one-parasitoid (1H1P) systems exhibit characteristic dynamics for such systems (e.g. in the absence of host self-limitation, the parasitoid over-exploits the host and drives the system to extinction, or highly chaotic systems which eventually result in biological extinction). Such regions are not detailed in these figures (*see* Lane *et al*. (1999) for a summary of such dynamics). Finally, variation on the axes in Figs. 1–4 is accomplished by varying the denominator of a ratio. Thus, decreasing the value of P's search efficiency or fecundity (Q's in Fig. 4) leads to increases in the value obtained on the abscissa or ordinate, respectively. This fact should be kept in mind when interpreting our results.

For the parameter value combinations used to generate Fig. 1, three-species coexistence is possible, and is stable for all but a very small region of parameter space where it occurs (*see* inset to Fig. 1A). The point (1,1) marked with an "x" on the panels of Fig. 1 is of particular note, since it is the point where the search efficiencies and fecundities of the two parasitoids are identical, such that $a_P = a_Q \equiv a$ and $\beta_P = \beta_Q \equiv \beta$. Because the c's and k's of both parasitoids are also identical in this figure, this point indicates the scenario in which both parasitoids are identical in their strategies except for their order of attack (we refer to this as the *strict* (1,1) case). *A priori*, one would expect the clearly inferior competitor Q, which always loses when superparasitism occurs, to be competitively excluded by P. Yet this is not the case! Further, this result is independent of the ecological parameters of

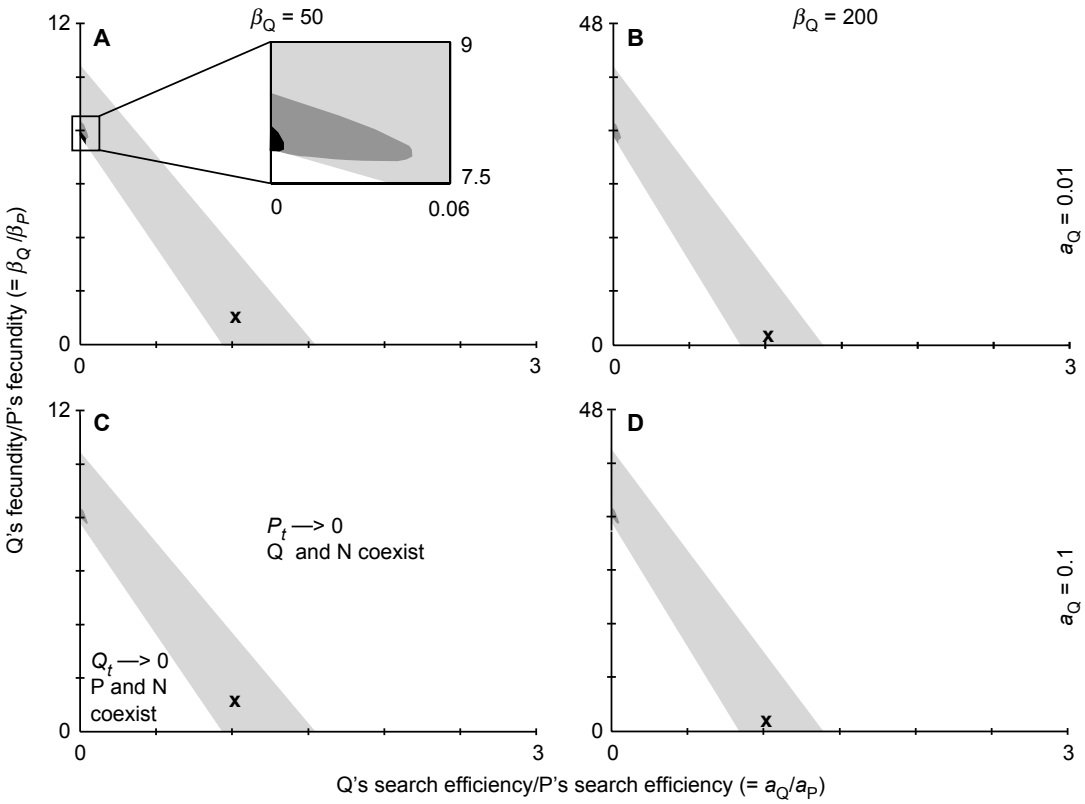

Fig. 1. Equilibrium stability diagrams for Eq. 1 as described in the text (incorporating Eqs. 2, 4 and 5, the DI scenario). All of the model parameter values except for the search efficiencies (a_P, a_Q) and fecundities (β_P, β_Q) are fixed. The values of the parameter a_Q and β_Q each take on the labeled values while a_Q and β_P vary on the abscissa and ordinate axes respectively. The host's density-independent growth rate λ = 1.1, the host is not self-limited (DI scenario), the parasitoid survival-and-sex-ratio parameters $c_P = c_Q = 0.2$, and the parasitoid aggregation parameters $k_P = k_Q = 0.25$. Each point in a given pane is shaded to indicate the qualitative outcome of a dynamical simulation of Eq. 1 for the parameters in question. Specifically, white represents regions of competitive exclusion following the pattern labeled in pane **C**, light gray regions indicate stable (equilibrium) three-species coexistence, dark gray regions indicate unstable (oscillatory) three-species coexistence, and black regions indicate uncontrolled host growth. The symbol "x" marks the point (1,1) on each pane.

the host (Fig. 2). Fecundity- and search-efficiency-equivalent competitors (i.e. the (1,1) case, but not necessarily strict if the parasitoids differ in their aggregation or sex ratio) stably coexist, particularly when the values of the parasitoid aggregation parameters (k_P and k_Q) create an additional distinction between the two parasitoid populations, as will be shown in the following sections. In general, when parasitoid aggregation is not high (e.g. k_P, $k_Q \geq 0.75$, unlike the situation depicted in Fig. 1), increasing a or β or both is destabilizing for the (1,1) case. This effect can potentially be offset if the host's intrinsic rate of increase (λ) is increased (under some circumstances by even as little as 10% or less), and/or if the strength of host density dependence is increased (K reduced), but the ability of these alterations to offset destabilization in this way depends on the values of the other parameters. Note, however, that under some circumstances increases in the host's intrinsic growth rate and/or strength of density dependence can act to *destabilize* the three-species equilibrium in the (1,1) case, in favor of two-species coexistence (which can be stable or unstable), or the extinction of both parasitoids.

From a comparison of panels A and B, or C and D, in Fig. 1 it is apparent that increasing

β_Q from 50 to 200 has only a small effect on the shape and relative size of the stability region, although the small black-shaded region of uncontrolled host growth disappears in the case a_Q = 0.01 (panel A). Finally, note the location of the areas of oscillatory coexistence and (in the case of Fig. 1A) uncontrolled host growth, abutting the ordinate axis. Values on the axes correspond to one of two scenarios: on the abscissa, the value of β_P is infinite, so that P's encounter rate is actually represented by $\varepsilon_P = a_P P$; on the ordinate, the value of a_P is infinite, so that P's encounter rate is actually represented by $\varepsilon_P = \beta_P P/N$ (*see* Lane *et al*. 1999). An encounter rate of the form $\varepsilon_P = \beta_P P/N$ is extremely destabilizing, and in one-parasitoid systems often leads to uncontrolled host growth (Getz & Mills 1996). Thus it is to be expected that, in regions where P's search efficiency and fecundity are high relative to Q's, so that Q is close to being unable to maintain itself in the system, and where the effect of P's search efficiency on stability diminishes ($a_P \rightarrow \infty$), the stability of the three-species system would be diminished, leading even to uncontrolled host growth under some circumstances (e.g. Fig. 1A). The size of such regions in parameter space increases with increasing instability due to decreased parasitoid aggregation, and decreases with increasing stability due to host density dependence, as will be illustrated below. Note that, on the ordinate axis itself, where P's search efficiency is never limiting, 1H1P systems are often unstable (Getz & Mills 1996).

Host strategies: population growth rate and self-limitation

Figure 2 illustrates the basic consequences of changes in the life-history strategy of the host for the stability of Eq. 1. In Fig. 2A and B the host's population growth rate has been increased from 1.1 to 2.0 (compare with panels C and D in Fig. 1), producing a large increase in the space occupied by simulations exhibiting three-species stable coexistence (note the abscissa scale). Also, the small area of oscillatory coexistence has been eliminated in favor of equilibrium coexistence. In addition, there is now a large difference in the proportion of coexistence parameter space as a function of Q's fecundity, unlike for the smaller value of λ. These two panes are essentially identical to those produced for a_Q = 0.01 (data not shown).

Going from density-independent to self-regulated population growth with K = 1000.0 (λ = 1.1 — compare Fig. 2C and 2D with 1A and 1C), the resultant changes in dynamics are rather small, most notably that the area of oscillatory coexistence is converted to equilibrium coexistence because of the stabilizing effects of host self-limitation.

Finally, when the host's population growth rate is increased from 1.1 to 2.0 and the host is self-limited with K = 1000.0, there is still an increase in stable parameter space due to the increase in the host's population growth rate (compare Fig. 2E with Fig. 1C), but it is diminished by the effect of density dependence (compare Fig. 2E with Fig. 2A). This diminishing effect is not complete, however, as can be observed by comparing Fig. 2F (K = 80.0) with Fig. 1C.

Parasitoid strategies: attack aggregation

The consequences of changes in attack aggregation are illustrated in Fig. 3A–E for the density-independent host-growth case, and in Fig. 3F–H, for the self-regulated host-growth case. If the parasitoid that attacks first is more aggregated (k_P: 0.25 $\rightarrow$ 0.75, compare with Fig. 2A; note that λ = 2.0 for panels A–C in Fig. 3), then the area of parameter space supporting coexistence decreases, while the proportion of this area associated with oscillatory coexistence increases. Furthermore, this destabilizing effect is asymmetrical with respect to the two parasitoids in at least three ways. First, in comparing Fig. 3A with Fig. 2A, it should be noted that all of the loss of coexistence parameter space occurs on the side of this region of parameter space closest to the origin, thus representing an increase in the area of parameter space in which P is able to exclude Q. In considering the two-species system, it was determined that increasing k_P from zero to unity led to an increase in stable parameter space, and that the system was stable for increasingly large values of λ (Lane *et al*. 1999). The consequences

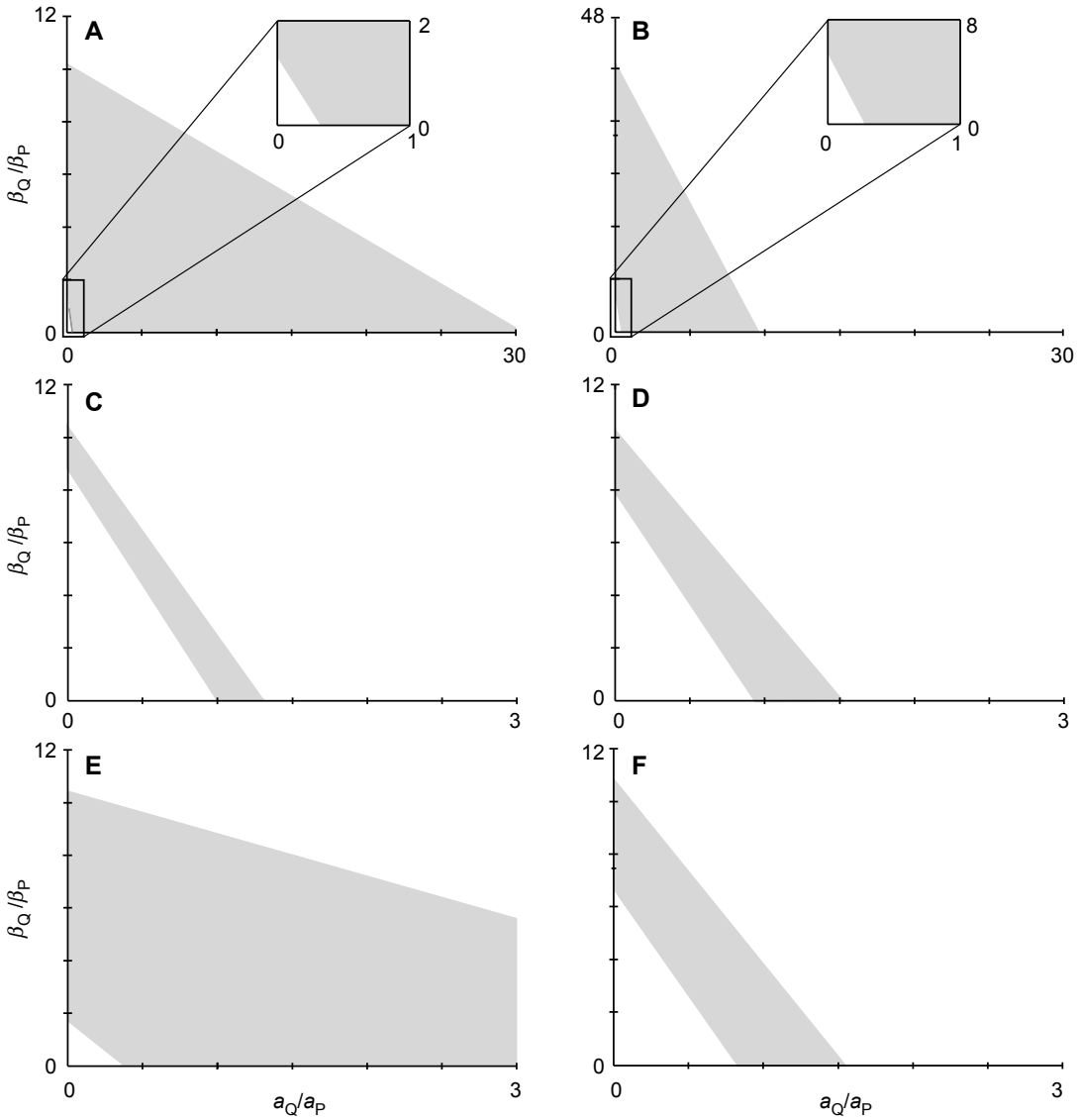

Fig. 2. Equilibrium stability diagrams for Eq. 1, as in Fig. 1 but incorporating an increased host *per-capita* growth rate (λ = 2.0, panes **A** and **B**); increased host density-dependence (the DD scenario, Eq. 3 with K = 1000.0, panes **C** and **D**); or both (panes **E** and **F**). Parameter combinations are as follows (all parameter values are as in Fig. 1 unless otherwise noted): — **A**: λ = 2.0, a_Q = 0.1, β_Q = 50.0; — **B**: λ = 2.0, a_Q = 0.1, β_Q = 200.0; — **C**: K = 1000.0, a_Q = 0.01, β_Q = 50.0; — **D**: K = 1000.0, a_Q = 0.1, β_Q = 50.0; — **E**: λ = 2.0, K = 1000.0, a_Q = 0.1, β_Q = 50.0; — **F**: λ = 2.0, K = 80.0, a_Q = 0.1, β_Q = 50.0.

of these facts are seen here. Decreasing aggregation (k_P: 0.25 → 0.75) and decreasing fecundity limitation (increasing β_P) serve to stabilize the N-P system relative to the N-Q system, and thus P is able to exclude Q from the three-species coexistence system for lower values of a_P and β_P.

Second, while the size of the three-species coexistence region shrinks in favor of N-P systems, three-species systems with higher values of a_P and β_P become unstable, as equilibrium coexistence is converted to oscillatory coexistence. This arises because, in 1H1P models, increasing aggregation causes exponential damping to switch to oscillatory damping.

Third, the magnitudes of these effects are asymmetrical with respect to the two parasitoids,

as can be seen in Fig. 3B, where k_Q is increased to 0.75. The proportion of parameter space given over to coexistence is dramatically reduced in favor of N-Q systems (note the abscissa scale), and the proportion of coexistence parameter space given over to oscillatory coexistence dramatically increases.

When both parasitoids have their attack aggregation reduced ($k_P = k_Q = 0.75$) the destabilizing effect is extreme (Fig. 3C). Coexistence parameter space is greatly reduced in favor of both N-P and N-Q systems, the stable proportion of coexistence parameter space is dramatically reduced (due mainly to the reduction in attack aggregation of parasitoid Q), and a large proportion of parameter space is now given over to uncontrolled host growth, because increasingly oscillatory solutions lead to systems wherein both parasitoids together are unable to control the host.

In a one-parasitoid system coexistence is not possible if the aggregation parameter $k > 1$ unless the host exhibits density dependence. Thus, it makes sense to ask if a parasitoid that exhibits little aggregation ($k > 1$; Fig. 3D and E) can invade a coexisting host–parasitoid system that does not include host density dependence (i.e. a system in which the resident parasitoid population's $k < 1$). For $k_p > 1$ the region of parameter space in which Q is excluded by P is greatly increased over its size for lower k_p values, and the size of the P-Q oscillatory coexistence region is increased and its position is on the side of the coexistence region adjacent to the N-P system region (compare Fig. 3D with Fig. 3A, and with Fig. 2A). Additionally, the region of coexistence parameter space is modified as a result of changes in Q's fecundity (compare Fig. 3E with Fig. 2B). The absolute size of the P-Q coexistence region shrinks, and the relative proportion of oscillatory coexistence parameter space to total coexistence parameter space is increased. No such modifications occur as a result of changes in Q's search efficiency (data not shown). It is worth emphasizing, however, that there is a large region of stable three-species coexistence, thus indicating that attack aggregation sufficient to stabilize a one-parasitoid system is also sufficient to stabilize a two-parasitoid system that would otherwise be unstable if the more aggregated parasitoid is removed.

Finally, the interaction between density dependence and reduced parasitoid aggregation can also be assessed (Fig. 3F–H), where, in comparing panel F with panel B in Fig 3, we see that density dependence reduces both the absolute size of the coexistence region and the oscillatory proportion when only Q has its aggregation reduced. (Note that $k_Q = 0.75$ for Fig. 3F–H; when only *P* has its aggregation reduced in the density-dependent case the reduction in coexistence parameter space is quite significant, but there is essentially no change in the proportion of the coexistence region which is composed of oscillatory coexistence — data not shown.) A comparison between panels G and C in Fig. 3 indicates that when both parasitoids have their attack aggregation reduced, the oscillatory proportion of the coexistence region is decreased, the uncontrolled host-growth portion is eliminated entirely, and the total size of the coexistence region decreases. Furthermore, when Q's search efficiency is reduced (Fig. 3H) the coexistence region is overall reduced, but the oscillatory part is eliminated completely. No such change takes place in the density-independent case, and there are essentially no changes to the outcomes shown in Fig. 3F–H resulting from changes to Q's fecundity (data not shown). Thus, when the aggregation of both parasitoids is reduced and the host is not self-limited, the effect is generally destabilizing. Three-species coexistence is enhanced if one of the parasitoids has high aggregation, as compared with the situation wherein both parasitoids have moderate aggregation. Under those circumstances the addition of host self-limitation leads to increased stabilization of the coexistence region, but the overall size of the region shrinks, as was shown previously for the case with high parasitoid aggregation.

Reversing the attack timing of resident and introduced parasitoid

In Figs. 1–3 variation along an axis corresponds to varying the denominator of the ratio defined variables (i.e. to varying the search efficiency, in the case of the abscissa, or fecundity, in the case of the ordinate, of P, the parasitoid attacking first in the host's life-cycle). In Fig. 4 the ratios have been inverted, so that variation on the axis

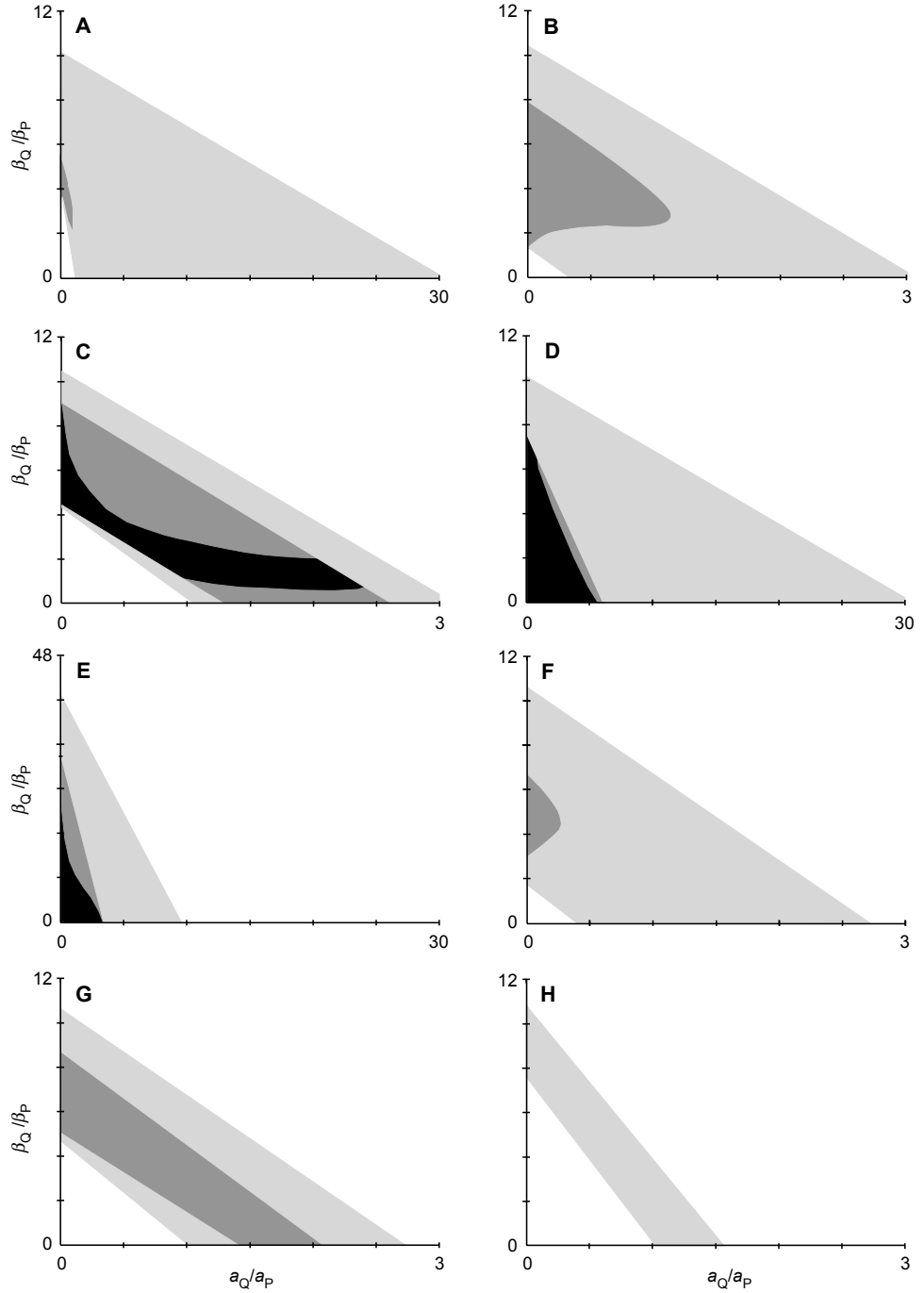

Fig. 3. Equilibrium stability diagrams for Eq. 1 as in Fig. 2A (λ = 2.0 and the DI scenario, panels **A**–**E**), or Fig. 2E (λ = 2.0 and the DD scenario, panels **F**–**H**), but with decreases in parasitoid aggregation (i.e. increases in the value of the aggregation parameter k) for one or the other or both of the parasitoids. Parameter combinations are as follows (parameter values for panes **A**–**E** are as in Fig. 2A, and for panes **F**–**H** as in Fig. 2E, unless otherwise noted): — **A**: a_Q = 0.1, β_Q = 50.0, k_P = 0.75, k_Q = 0.25; — **B**: a_Q = 0.1, β_Q = 50.0, k_P = 0.25, k_Q = 0.75; — **C**: a_Q = 0.1, β_Q = 50.0, k_P = 0.75, k_Q = 0.75; — **D**: a_Q = 0.1, β_Q = 50.0, k_P = 2.0, k_Q = 0.25; — **E**: a_Q = 0.1, β_Q = 200.0, k_P = 2.0, k_Q = 0.25; — **F**: a_Q = 0.1, β_Q = 50.0, k_P = 0.25, k_Q = 0.75; — **G**: a_Q = 0.1, β_Q = 50.0, k_P = 0.75, k_Q = 0.75; — **H**: a_Q = 0.01, β_Q = 50.0, k_P = 0.75, k_Q = 0.75.

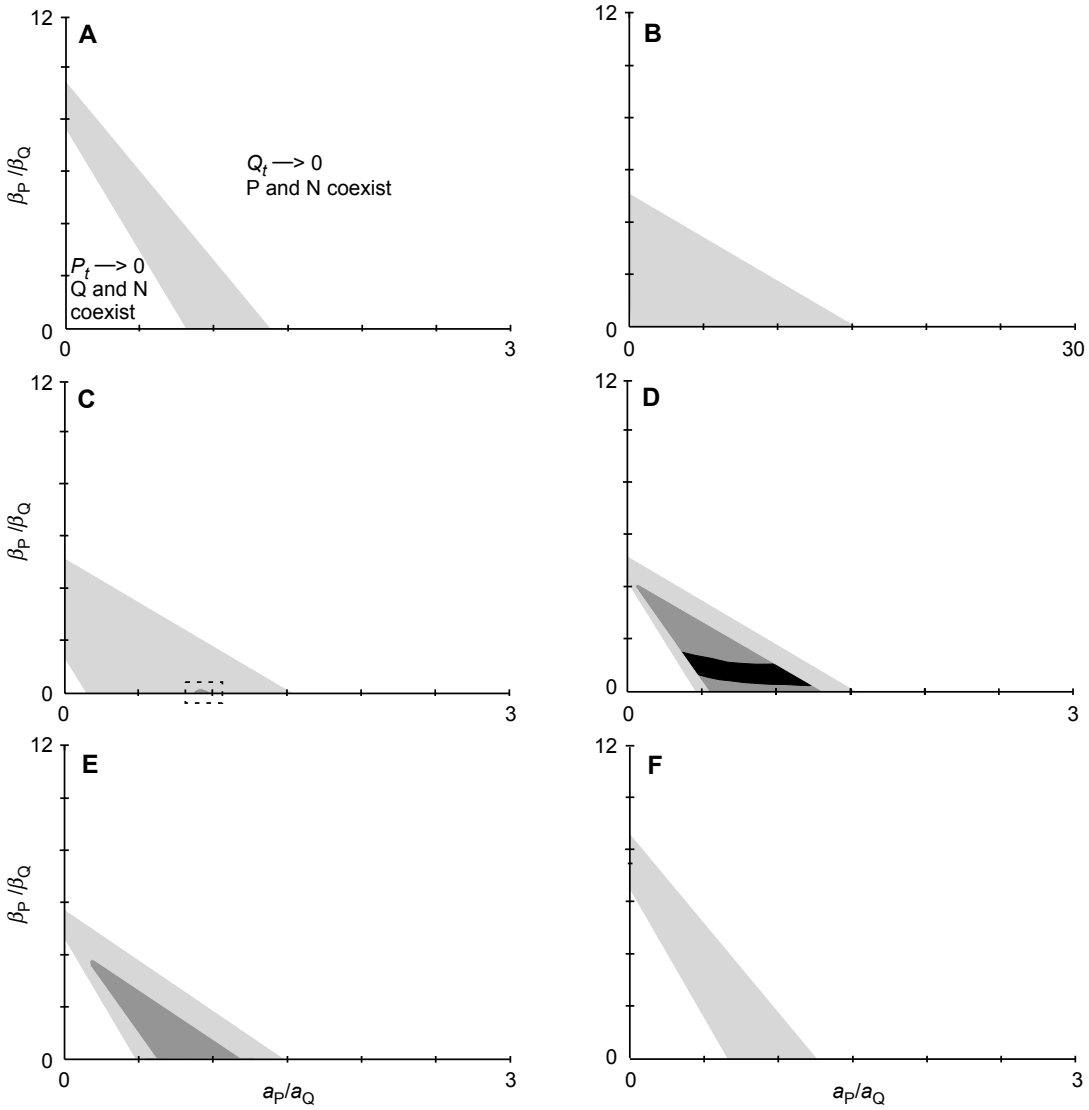

Fig. 4. Equilibrium stability diagrams for Eq. 1 with parasitoid *Q*, the parasitoid attacking second, as the resident. **A**: Conditions as in Fig. 1C; **B**: Conditions as in Fig. 2A; as a consequence of the reversal of the resident and invader roles, the fixed parameter values in panes **A**–**B** are reversed between the two parasitoids from those in Figs. 1–2 — in particular, $a_Q = a_R = 0.1$. **C**–**F**: $\lambda = 2.0$, $\beta_P = 50.0$, $c_P = c_Q = 0.2$, $k_P = 0.75$; **C**–**D**: $K \rightarrow \infty$ (the DI scenario); **E**–**F**: $K = 1000.0$ (the DD scenario); **C**: $a_P = 0.1$, $k_Q = 0.25$; **D**, **E**: $a_P = 0.1$, $k_Q = 0.75$; **F**: $a_P = 0.01$, $k_Q = 0.75$.

is accomplished by variation in the search efficiency or fecundity of Q, the parasitoid attacking second.

Attacking second is clearly a disadvantage (Fig. 4A and B). Individuals in population Q require a higher search efficiency, fecundity or both to successfully invade a stable N-P system than individuals in population P do to successfully invade a stable N-Q system (compare Fig. 4A with Fig. 1C); this effect is increasingly pronounced with increases in host population growth rate (compare Fig. 4B with Fig. 2A). Also, reversing the attack timing of resident and introduced parasitoids eliminates the small regions of oscillatory coexistence in the cases where the host population growth rate is low.

The consequences of changes in P's search efficiency and fecundity for the coexistence region are essentially identical to those in the $k_P = k_Q = 0.25$ cases previously considered (data not shown).

The effects of changes in parasitoid aggregation and the addition of host self-regulation are illustrated in Fig. 4C–F. The most significant effect of decreasing P's aggregation parameter compared with that of Q's is a reduction in coexistence parameter space (compare panels B and C in Fig. 4). Comparing Fig. 4C directly with Fig. 3B illustrates the asymmetrical effect of the attack ordering: the coexistence region is greatly reduced, but the region of oscillatory coexistence is almost eliminated (the dashed-line box in Fig. 4C highlights the small remaining bit). Decreasing the resident's aggregation has a much greater destabilizing effect on the coexistence region when the resident attacks second, although the coexistence region as a whole is larger. Note that coexistence parameter space is also reduced when it is the introduced parasitoid's aggregation that is decreased (data not shown), but that there is no corresponding change in oscillatory coexistence — all coexistence is equilibrial under these circumstances, irrespective of the identity of the resident.

Reducing parasitoid aggregation in both parasitoids is extremely destabilizing, irrespective of which parasitoid is the invader (compare Fig. 4D with 3C). The addition of host self-regulation acts as a stabilizing influence with respect to uncontrolled host growth, but has less of an impact on oscillatory coexistence (Fig. 4E: compare with Fig. 3G for the consequences of reversing the attack timing of resident and invader; compare with Fig. 3C for the effects on uncontrolled host growth and oscillatory coexistence). Finally, reducing the resident's search efficiency when hosts are self-limiting eliminates oscillatory coexistence and modifies the relationships between parasitoid fecundities and search efficiencies, which permit three-species coexistence (Fig. 4F: compare with Fig. 3H for the consequences of reversing the attack timing of resident and invader; compare with Fig. 4E for the effects on uncontrolled host growth and oscillatory coexistence).

Consequences for host suppression

For simulations resulting in stable three-species equilibria it is possible to measure the increase in host suppression resulting from the addition of a second parasitoid to a 1H1P system at equilibrium. Because this one-parasitoid system provides the initial conditions for all the three-species simulations, using the variable $q_{PQ} = N^*_{PQ}/N^*$ (where N^*_{PQ} is the host population's equilibrium density in the presence of both parasitoids, and N^* is the host's equilibrium density in the presence of the resident parasitoid only; Beddington *et al.* 1975, Hassell 1978) is a natural approach for comparing the effect of two parasitoids on host suppression to that of one alone. Note that $q_{PQ} = 0$ represents complete host suppression while $q_{PQ} > 1$ represents a *release* of the host from parasitism.

One significant consequence of the change in N^* as a function of changes in the resident parasitoid's parameter values is that, as the resident's fecundity increases, the amount of additional suppression provided by a second parasitoid *decreases* (i.e. q_{PQ} goes from zero toward unity; Fig. 5A). This follows because increases in the resident's fecundity lead to increased host suppression by this parasitoid alone (i.e. lead to decreases in N^*), so that the ability of a second parasitoid of a given fecundity to further reduce the host equilibrium decreases (i.e. q_{PQ} increases with β_R). When the fecundity of the *resident* remains fixed, increases in the *introduced* parasitoid's fecundity lead to increases in host suppression (Fig. 5B). These relationships also hold true for the search efficiency and attack aggregation parameters of the parasitoids (data not shown). Increases in the value of any one of these three parameters in the resident result in decreasing the amount of additional host suppression provided by the introduced parasitoid; increases in the value of any one of these three parameters in the introduced parasitoid result in increasing the amount of additional host suppression provided by the introduced parasitoid.

There is a small asymmetry to the above effect as a function of whether the resident attacks first or second in the host's life-cycle. This arises because of the relationship between the fecundi-

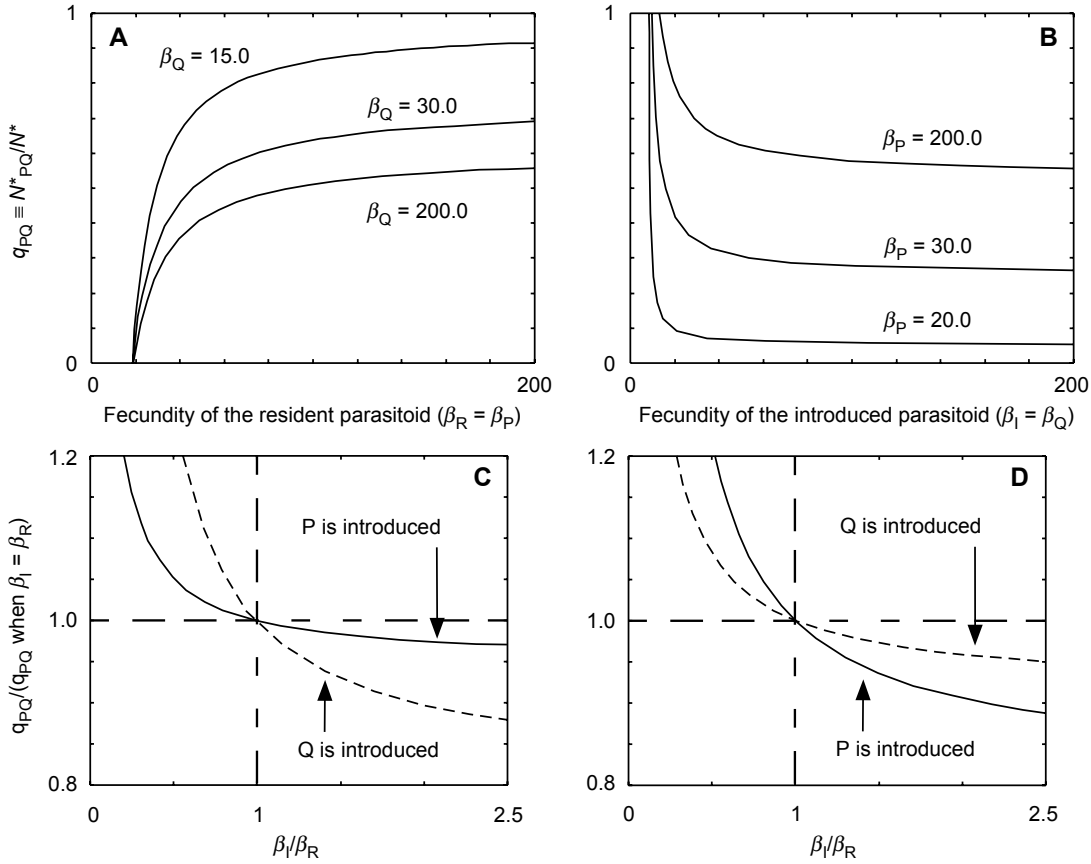

Fig. 5. A–B: The relationship between parasitoid fecundity, β_P (panel **A**), and β_Q (panel **B**), and q_{PQ}, the degree of additional host equilibrium suppression provided by the introduction of a second parasitoid population, for three different values of the fecundity of the other parasitoid, β_Q (panel **A**), and β_P (panel **B**). Values of q_{PQ} less than unity indicate additional host equilibrium suppression due to the presence of the second parasitoid population in the system ($a_P = a_Q = 0.1$). **C–D**: The relationship between the ratio of the two parasitoids' fecundities and the consequences of changes in this ratio for host equilibrium suppression. **C**: Increases in the fecundity of the introduced parasitoid relative to that of the resident produce more marginal host suppression if the introduced parasitoid attacks later ($a_P = a_Q = 0.1$). **D**: The situation is reversed when $a_Q < a_P$, such that increases in the fecundity of the introduced parasitoid relative to that of the resident produce more marginal host suppression if the introduced parasitoid attacks earlier ($a_P = 0.1$, $a_Q = 0.01$). **A–D**: $c_P = c_Q = 0.2$, $k_P = k_Q = 0.25$, $K = 1000.0$, $r = 2.0$.

ties of the two parasitoids and the timing of their attacks in the host's life-cycle, the basic nature of which is altered by the relative values of the parasitoid's search efficiencies and degree of attack aggregation. Consider the situation where all the parameter values of the two parasitoids except for their fecundities are equal, so that the only differences between them are their fecundities and timing of attack in the host's life-cycle. Under these circumstances, if the introduced parasitoid attacks later than the resident in the host's life-cycle and has a higher fecundity than the resident, slightly greater marginal host suppression occurs (i.e. the difference between the host's equilibrium densities in the presence of one versus two parasitoids will be greater) than if the introduced parasitoid attacks earlier than the resident. The converse also holds (Fig. 5C). Thus, all else being equal, if a second parasitoid is to be introduced, and it attacks after the resident, it should have a higher fecundity than the resident to achieve greater additional host suppression. If it attacks earlier, it should have a lower fecundity than the resident. This is essentially a manifestation of the disadvantage of attacking second, and it should be noted that in general the amount

of this asymmetry is relatively small. It can be magnified, and the difference in degree of additional suppression increases, as the fecundity of the resident decreases, as the amount of attack aggregation in *both* parasitoids decreases (i.e. k_P and k_Q both get larger), and/or as the host's intrinsic growth rate increases. The strength of host self-limitation does not alter the relative nature of this asymmetry, nor does changing the search efficiencies of *both* parasitoids together (i.e. a_P and a_Q both increase or both decrease). The asymmetry can be *reversed*, however, if the parasitoid attacking second has a search efficiency sufficiently less than that of the parasitoid attacking first (i.e. $a_Q < a_P$). It can also be reversed if the degree of attack aggregation of the parasitoid attacking second is sufficiently greater than that of the parasitoid attacking first (i.e. $k_Q < k_P$, recall that larger k means less aggregation), where in both cases "sufficiently" depends on the values of the other parameters. Under these last two sets of circumstances, if the introduced parasitoid attacks later than the resident in the host's life-cycle, and has a higher fecundity than the resident, there will be less marginal host suppression than if the introduced parasitoid attacks earlier than the resident (Fig. 5D). The converse also holds. Note that these last two features can compensate for each other. If $a_Q < a_P$ but $k_Q > k_P$, or vice versa, again by sufficient amounts, then the asymmetry will be maintained as described initially (e.g. as in Fig. 5C).

It is important to recognize that there can be a conflict between the properties of a 1H2P system that provide the maximal *absolute* host suppression, and those properties that provide the maximal *additional* host suppression resulting from the presence of the second parasitoid. Thus, the addition of a second parasitoid to a 1H1P system *at equilibrium* for purposes of a strong increase in host suppression can be justified under several sets of circumstances. In general, systems with high host population-growth-rates and low host self-regulation will allow a second parasitoid to substantially increase host suppression. Furthermore, high attack aggregation in the resident allows the opportunity for an introduced parasitoid to greatly improve host suppression. The degree of aggregation in the introduced parasitoid is less important.

Discussion

The ecological analysis of multiparasitoid systems has been motivated by two considerations. The first is that such systems are widely found in nature (Hutson & Law 1985). Many, perhaps most, hosts of parasitoids support more than one parasitoid species, a significant fraction of which are specialists on that host. The second relates to the benefit or detriment of introducing more than one enemy species in classical biological control.

With respect to the first issue, our results suggest that *stable* three-species coexistence is possible under a wide range of conditions, provided *at least one* (and not necessarily both) of the parasitoids has sufficient attack aggregation ($k < 1$). In particular, attack aggregation sufficient to stabilize a one-parasitoid system can be sufficient to stabilize a two-parasitoid system that would otherwise be unstable if the more aggregated parasitoid is removed. On the other hand, when the search efficiency *and* fecundity of one of the parasitoid populations is much lower than the other, it is likely to be competitively excluded.

Our results indicate that parasitoids on the same host can coexist even when the search efficiencies or fecundities of the two parasitoid populations are widely (i.e. orders of magnitude) different, provided one is more efficient and the other more fecund. This is in agreement with May and Hassell (1981), indicating that the presence of fecundity limitation does not necessarily adversely affect the potential for stable coexistence.

While attacking second is clearly disadvantageous, our results suggest that this disadvantage is not as serious an impediment as one might think from analyses of two competitors exploiting a single non-replaceable resource (Tilman 1990, Briggs 1993), particularly when parasitoid heterogeneity is high (i.e. k_P, $k_Q < 1$). Circumstances are known to exist under which competitive exclusion is weakened (Armstrong & McGehee 1980, Getz & Schreiber 1999). In particular, coexistence can in general occur when the two predator or parasitoid populations utilize different stages of the host population's life-cycle (Haigh & Maynard Smith 1972, Briggs

1993, Briggs *et al*. 1993), as is the case under the interpretation of Eq. 1's structural distinction between the two parasitoid populations. In addition, coexistence may be expected when there are time-lags in the dynamics (Hutchinson 1961, Stewart & Levin 1973, Koch 1974), as is the case in discrete-time models representing synchronized host-parasitoid generations (Mills & Getz 1996). As Briggs *et al*. (1993) note, even Tilman's R^* concept (1982, 1990) allows for multispecies coexistence in a patchy environment, although it requires multiple resources, each species having a different limiting resource-ratio. Under the circumstances described by Eq. 1, if the parameters of P and Q are the same, then R^* is the same for both parasitoids, but coexistence nonetheless occurs (i.e. the strict (1,1) scenario). Even if the parasitoid parameters are perturbed to a lesser or greater degree, thus changing the R^* of one or the other of the parasitoids, coexistence will still occur in general. Thus, the generalization that the stronger competitor will draw down the resource to the point of excluding the weaker (i.e. the R^* rule) does not apply under these circumstances.

One general way in which coexistence is enhanced is through the presence of stabilizing features in the model (Armstrong & McGehee 1980, May & Hassell 1981, Briggs 1993, Mills & Getz 1996). In particular, the introduction of nonlinearities in the growth rate of the host (self-limitation) and/or the parasitoids (attack aggregation) increase the amount of parameter space given over to coexistence, and decrease the proportion of the coexistence region given over to oscillatory coexistence in favor of equilibrial coexistence. It is important to recall, however, that host density dependence, while eliminating oscillatory coexistence in favor of equilibrial coexistence, decreases the range of parasitoid search efficiency and fecundity ratios which permit coexistence at all. This effect is more pronounced with increases in the host population's intrinsic growth rate, and it occurs regardless of the degree of attack aggregation in either parasitoid, although it is mitigated by increased parasitoid attack aggregation. As has been observed previously in the one-parasitoid population case (Hochberg & Lawton 1990, Taylor 1993, Getz & Mills 1996), increasing aggregation does not always lead to increased stability. Hochberg and Lawton (1990) found that, in 1H1P systems, as the strength of host density-dependence increased, the importance of increased parasitoid aggregation for stability decreased. In fact, they found that in systems where the strength of host density-dependence leads to chaotic dynamics, *decreased* levels of parasitoid aggregation were necessary to stabilize the interaction. In the 1H2P case, however, over the range of aggregations (k values) examined in our study, this is not the case. Increased parasitoid aggregation in one or both parasitoids (but somewhat more-so in the parasitoid attacking first) always leads to increased coexistence parameter space overall, and to an increased proportion of equilibrial coexistence parameter space.

As can be seen clearly from the one-parasitoid cases (Getz & Mills 1996, Lane *et al*. 1999), fecundity-limitation is generally a destabilizing feature for host–parasitoid model dynamics, because the proportion of hosts the parasitoids are able to attack decreases as host density increases (the saturating feature of Holling Type II functional responses; Murdoch & Oaten 1975). The nonlinearities in host and parasitoid population growth rates are stabilizing because they provide negative feedback to the population growth rates in response to changes in population density. Fecundity limitation serves to reduce the strength of this negative-feedback linkage for each parasitoid, so that when more than one parasitoid is present in the system, increased aggregation offsets fecundity limitation's destabilizing effects.

Much of the work modeling host–parasitoid interactions has focused on the need and potential for stable coexistence equilibria (Barlow & Wratten 1996, Mills & Getz 1996). This emphasis stems from the perceived need for these systems to respond in a density-dependent fashion to externally-induced perturbations. If this does not occur (i.e. if there are no negative feedbacks), all populations will eventually achieve zero density via stochastic random walk (Cole 1960). The need for a stable equilibrium to provide continued coexistence is no longer accepted *a priori*. Many workers have clearly demonstrated theoretically that oscillatory but bounded population-density trajectories

can occur as a result of spatial and/or temporal variability (Koch 1974, Armstrong & McGehee 1980, Briggs 1993, Briggs *et al.* 1993). It has also been argued that biological control systems in particular need not necessarily exhibit stable equilibria for persistence and may in many cases be characterized by local extinctions and subsequent recolonizations from source populations (Murdoch *et al.* 1985, Comins & Hassell 1996, Murdoch & Briggs 1996). As the analysis in this study demonstrates, a variety of conditions exist under which persistent but oscillatory three-species coexistence occurs. Such coexistence occupies an increasing proportion of the total coexistence parameter space as stabilizing features of the dynamics are weakened (i.e. aggregation decreases or host density-dependence is absent). It is also the case, however, that in a non-spatially-structured environment with no source populations, as is represented by the model analyzed here and as is the case in classical biological control introductions, oscillatory populations would be more vulnerable to extinction as a result of stochastic factors (e.g. environmental perturbations). Thus, while it is clear that non-equilibrial coexistence is possible, it is also clear that, given the possibility of equilibrial coexistence, the latter will enhance the probability of continued three-species coexistence. This is a particular consideration in classical biological control, which we examine next.

Our analysis supports May and Hassell's (1981) finding that, when it comes to host suppression, more parasitoids are in general better. While it has been clearly shown that this prediction is robust with respect to discrete-time models, it often fails to hold up when systems with overlapping generations are modeled, particularly when age or stage structure in the host population is incorporated into the model (Briggs 1993, Briggs *et al.* 1993). Thus, the generality of this prediction should remain confined to systems in which the host and parasitoid populations are synchronized.

May and Hassell (1981) found that increasing the host population's growth rate led to decreased host suppression. Our analysis supports exactly the opposite contention: increasing the host population's growth rate leads to increased host suppression. Clearly when parasitoids are fecundity limited, increasing the reproductive rate of the pest permits an increased numerical response in the parasitoids. In the case of Eq. 1, this increase more than compensates for the host increase, which is ultimately limited by environmental factors, thereby resulting in the host's equilibrium density decreasing with increasing λ in the presence of the parasitoids. This is in clear contrast to the situation when fecundity is not limiting (May & Hassell 1981, Hochberg & Lawton 1990; but *see* Ives & Settle 1996), in which case increases in the pest's reproductive rate lead to *decreases* in the ability of the parasitoids to suppress the host (i.e. the host's equilibrium density increasing with increasing λ in the presence of the parasitoids).

Decreased host equilibrium density results from decreased host self-regulation, and from increased parasitoid search efficiency in the invading parasitoid. It is also worth pointing out, however, that the same does not apply with respect to parasitoid fecundity. In the one-parasitoid case, decreased parasitoid fecundity can lead to an increase in host equilibrium density (Lane *et al.* 1999). In the two-parasitoid case, increased host equilibrium densities result not from decreased fecundity in the invading parasitoid, but from *increased* fecundity in the resident parasitoid. Thus, as the resident parasitoid's fecundity goes down, so does the host equilibrium density. This may be due to the ability of the invading parasitoid to better control the host on its own due to its extremely high search efficiency and fecundity. Under such circumstances, low fecundity in the resident parasitoid may be desirable because it prevents the resident parasitoid from interfering (i.e. through multiparasitism) with the more effective control provided by the invader, and/or allows the control provided by the resident to more effectively compliment that of the invader. Godfray and Waage (1991), however, have shown that density dependence in both parasitoid populations (in the form of mutual interference) can allow two parasitoid populations to more effectively reduce the density of the host population than either parasitoid by itself. Higher fecundity in the parasitoid populations increases the degree of mutual interference (intraspecific competition) via superparasitism. The current result is thus at odds with that

of Godfray and Waage (1991). This discrepancy will require further investigation to resolve.

The demonstration that a parasitoid population with attack aggregation sufficient to stabilize a one-parasitoid system can stabilize a two-parasitoid system that would otherwise be unstable indicates that multiparasitoid systems may be widely found in nature precisely because they are ecologically and evolutionarily favored over 1H1P systems. This bodes well for the long-term, stable biological control of insect pests in multiparasitoid systems, where single parasitoid introductions might otherwise fail, provided that parasitoids with complimentary combinations of life-history parameters to maximize absolute suppression can be identified.

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