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# Examining the Relative Importance of Spatial and Nonspatial Coexistence Mechanisms

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ABSTRACT: Much of the work on species coexistence has focused on the presence or absence of single mechanisms. Most theoretical frameworks, however, do not allow one to measure the strength of coexistence mechanisms, and so it has been difficult to determine the relative importance of each mechanism when multiple mechanisms are present. We present a model inspired by the California red scale system, in which two parasitoids coexist on a single, tree-dwelling host-scale insect. Previous work suggests that coexistence may be promoted both by intraguild predation (IGP) and by differing preferences for hosts on stems versus hosts on leaves (habitat preference). By applying an analytic framework that quantifies the strengths of spatial coexistence mechanisms, we are able to measure the individual contributions of IGP, habitat preference, and their interaction to maintaining coexistence. We find that habitat preference is much more effective at promoting coexistence in this model than in IGP. Furthermore, the effects of habitat preference and IGP are not independent. When the two parasitoids prefer different habitats, the coexistence-promoting effects of habitat preference are strengthened by IGP if IGP gives a moderate advantage to the inferior competitor. If IGP either confers an excessive advantage or favors the superior competitor, it can diminish the coexistence region.

*Keywords:* coexistence, competition, intraguild predation, habitat preference, California red scale, parasitoid.

Theoretical ecologists have put a great deal of effort into examining the details and dynamics of single mechanisms

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of coexistence, while multiple concurrent mechanisms have only recently begun to receive attention (Chesson 2000a; Levin 2000; Amarasekare et al. 2004). This focus on single mechanisms stems from obvious historical roots, yet the empirical literature has shown that in most real biological systems, several potential coexistence mechanisms occur. Here we use a simplified model to examine the interactions between spatial and nonspatial coexistence mechanisms as well as their relative dominance throughout parameter space. We direct our modeling efforts by focusing on coexistence in a real, simple, well-studied ecological system: California red scale and its parasitoids.

California red scale (CRS) is an introduced insect pest of citrus that can infest all aboveground parts of a tree, reduces fruit production, and can cause tree mortality in extreme infestations. CRS is maintained at extremely low, stable densities by resource-specialist parasitoids (DeBach et al. 1971). In our study groves, two parasitoids, *Aphytis melinus* (Debach) and *Encarsia perniciosi* (Tower), have coexisted since the 1950s (DeBach and Sundby 1963). *Encarsia* is an endoparasitoid that requires unparasitized hosts for successful development. *Aphytis* is an ectoparasitoid that can develop successfully from both parasitized and unparasitized hosts. Details of the biology of these species can be found in work by Ebeling (1959), Rosen and DeBach (1979), Baroffio (1997), and Borer et al. (2004). Current empirical evidence points to two mechanisms as the most likely to maintain parasitoid coexistence in this system: intraguild predation and spatial habitat preferences.

The first coexistence mechanism likely to play a role in this system, intraguild predation (IGP, also called facultative hyperparasitism in parasitoids), is a nonspatial interaction between parasitoids in which *Aphytis* reparasitizes a host containing a developing juvenile *Encarsia*. The juvenile *Aphytis*, acting as an intraguild predator, consumes the developing *Encarsia* (Borer 2002b). Theory has shown that when the intraguild prey is a better exploitative resource competitor, under some conditions IGP alone can maintain coexistence (Briggs 1993; Holt and Polis 1997). Laboratory observations have shown that *Encarsia* can par-

asitize a host more quickly than can *Aphytis*, and in CRS, *Encarsia* has a substantially higher per capita production of female progeny than does *Aphytis* (DeBach and Sundby 1963; Borer 2002*a*). Here, for simplicity, we use "IGP" as shorthand to refer to this balance between intraguild predation and resource exploitation that can act as a coexistence mechanism. Although field patterns suggest that IGP may promote coexistence of *Aphytis* and *Encarsia* (Borer et al. 2003), a biologically detailed model of IGP in the California red scale system suggests that IGP alone may not be sufficient (Borer 2002*a*; E. T. Borer, unpublished manuscript).

The second mechanism implicated in parasitoid coexistence in this system is habitat preference within a tree. Field observations and experiments have shown that when given a choice of red scale on leaves or stems, *Aphytis* chooses to exploit hosts on leaves at a much higher rate than those on stems (Borer et al. 2004). Aggregation in many forms has been shown to maintain coexistence (Klopfer and Ives 1997), and our current model demonstrates that aggregation maintained by spatial habitat preferences also can function to promote coexistence of resource competitors. Although theory demonstrates that, given the correct combination of parameter values, either mechanism alone could maintain coexistence, the potential role of each is not clear in the red scale system.

Here we use the red scale system as a jumping-off point to examine the conditions under which two very different coexistence mechanisms, IGP and spatial habitat preferences, should be most important for maintaining coexistence in ecological communities. We develop a model inspired by red scale, *Aphytis*, and *Encarsia* but use it to examine a much broader range of biologically interesting parameter values than those observed in the CRS community. We also investigate whether IGP and spatial habitat preferences contribute independently to coexistence or whether they interact with each other, producing a net effect that is greater or less than the sum of its parts. To accomplish this, we use the framework presented by Chesson (2000*a*), which allows us to quantify the contributions of IGP, habitat preference, and their interaction to coexistence. We find that these mechanisms have sometimes superadditive and sometimes subadditive effects on species growth rates, demonstrating that the interaction of multiple mechanisms in a community is not a simple additive process.

## Model

We use a discrete time lottery–type formulation to examine the interaction of coexistence mechanisms. Although the CRS community has traditionally been described using a continuous time delay/differential equation formulation,

the lottery approach gives us additional analytical ability while qualitatively reproducing the sizes of the coexistence regions given by a biologically detailed delay-differential equation model of IGP (Borer 2002*a*; E. T. Borer, unpublished manuscript). Our primary goal is to develop a framework for understanding the biological conditions under which habitat preferences and IGP will be most important in ecological communities. The formulation of our model is determined by the biology of the CRS system, but we examine combinations of parameter values that are unrealistic for that system. Thus, in the model formulation, we motivate parasitoid species 1 with *Aphytis* in mind and parasitoid species 2 with *Encarsia* in mind. However, in our examination of species coexistence ("Results"), we refer to the parasitoids as "species 1" and "species 2" to emphasize the generality of our findings to other ecological communities.

### Host Dispersal and Competition

The environment is divided into patches of leaf and stem. Adult red scale females are sessile, and red scale larvae disperse only a short distance. For simplicity, we assume that a proportion $\delta$ of dispersing larvae move from stems to leaves and vice versa while the rest are retained in their natal habitat type. The number of hosts on, for example, stem habitat after dispersal is thus

$$H'_s = (1 - \delta)H_s + \delta H_l, \tag{1}$$

where $H_s$ is the density of hosts born on a stem patch and $H_l$ is the density of hosts born on a leaf patch. We do not track host movements explicitly, so the density of hosts in one habitat type is the same across all patches of that type. The coexistence boundaries are not sensitive to low levels of host dispersal, and all of our figures will be shown for $\delta = 0$.

Red scale larvae compete for settlement sites after they disperse. We assume that hosts compete within a patch, leading to Ricker model growth in the absence of parasitoids. The density of hosts in habitat $x$ after competition is thus

$$H'_x e^{-\alpha H'_x},$$
$$x = s, l, \tag{2}$$

where $H'_x$ is the postdispersal density of hosts in habitat $x$ and $\alpha$ is the Ricker competition coefficient.

## Habitat Preference

Experimental work has shown that across an extremely broad range of CRS density, *Aphytis* prefers hosts on leaves over those on stems, although it is capable of parasitizing hosts in both habitats. *Encarsia*, in contrast, is more catholic in its host use among habitats (Borer et al. 2004). Because resource preferences from complete overlap to complete segregation have been observed in other communities (Manly et al. 1992), we model habitat preference in the following general way.

In contrast to the hosts, the two parasitoids are highly mobile. When the parasitoids emerge, we imagine them joining a common pool. We denote the proportion of patches that are stems by $p_s$ and the proportion that are leaves by $p_l$ and assume that the proportion of time that a parasitoid spends searching in habitat $x$ is $p_x E_{jx}$. In all of the figures in this article, we assume that there are equal amounts of stem and leaf habitat ($p_s = p_l = 0.5$); however, making the more realistic assumption that there is more leaf habitat than stem habitat does not qualitatively change our results ("IGP, Habitat Preference, and Their Interaction"). Note that if there is an equal amount of stem and leaf habitat, then the proportion of time spent in habitat $x$ is proportional to $E_{jx}$, species $j$'s affinity for habitat $x$. From this we find that $P_{jx}$, the number of species $j$ parasitoids in a patch of habitat type $x$, is $E_{jx}\overline{P_j}$, where $\overline{P_j}$ is the spatially averaged parasitoid density. We quantify the degree of habitat preference with the parameter $\beta_j = E_{jl}/E_{js}$, the ratio of the affinity for leaves to that for stems. When $\beta_j = 1$, there is no preference, and when $\beta_j$ is either small or large, there is a large preference. (Articles such as Manly et al. 1992 have quantified preference with a parameter $\alpha$ that is 0 when a species has a strong negative preference and 1 when it has a strong positive preference. Here, $\beta = \alpha/(1 - \alpha)$.) We assume that parasitoid $j$ oviposits at a constant rate $a_j$ without regard to the number of times that a host has been previously parasitized so that the number of times a host at location $x$ is parasitized by species $j$ follows a Poisson distribution with mean $\mu_{jx} = a_j E_{jx}\overline{P_j}$. Our results would be the same if instead of spending more time in a preferred habitat, a predator had a high attack rate there ("Analysis Using $\tilde{\lambda}'_i$, $\Delta N$, and $\Delta \kappa$").

The proportion of hosts parasitized zero times by species $j$ is $\exp(-\mu_{jx})$. The density of hosts in habitat $x$ after dispersal, competition, and parasitism by species 1 (*Aphytis*) and 2 (*Encarsia*) is thus

$$H'_x e^{-\alpha H'_x} e^{-\mu_{1x} - \mu_{2x}}. \tag{3}$$

The hosts that survive competition and parasitism reproduce with constant effective fecundity $F$ (the effective fecundity is the number of offspring produced that will survive the dispersal phase), so the local host dynamics are

$$H_x(t + 1) = FH'_x e^{-\alpha H'_x} e^{-\mu_{1x} - \mu_{2x}}. \tag{4}$$

## Intraguild Predation

*Aphytis* is an ectoparasite, and *Encarsia* is an endoparasite, and so if *Aphytis* and *Encarsia* oviposit in a host at roughly the same time, the *Aphytis* larva will consume both the scale and the *Encarsia* larva within, and an *Aphytis* adult will emerge; the ectoparasitoid is the intraguild predator, and the endoparasite is the intraguild prey. However, *Encarsia* is able to exploit earlier instars than *Aphytis*, and if *Encarsia* oviposits sufficiently in advance of *Aphytis*, then it can induce a pseudomolt, a hard covering rendering the scale invulnerable to further oviposition, and an *Encarsia* adult will emerge (Borer 2002b). To model this fully would require a stage-structured model, such as that of Briggs (1993) and Briggs et al. (1993). Here we subsume the details of this stage structure into $\eta$ and allow the species emergence to be determined by a biased lottery (Chesson and Warner 1981). In spite of this simplification, the current model produces coexistence regions similar in size to those of a biologically detailed model of this IGP interaction (Borer 2002a; E. T. Borer, unpublished manuscript). If there are $A$ species 1 (*Aphytis*) eggs laid in a host and $B$ species 2 (*Encarsia*) eggs, then the probability that a species 1 parasitoid will emerge is

$$P(1 \text{ emerges}|A, B; A + B \neq 0) = \frac{A}{A + \eta B}, \tag{5}$$

and the probability that a species 2 parasitoid emerges is 1 minus this or

$$P(2 \text{ emerges}|A, B; A + B \neq 0) = \frac{\eta B}{A + \eta B}. \tag{6}$$

This model, while inspired by the CRS community, is intended to generalize to other communities with omnivory. Thus, the bias parameter $\eta$ represents the advantage of the intraguild predator (ectoparasitoid) in a general way, making species 2 the ectoparasitoid if it is >1 and making species 1 the ectoparasitoid if it is <1. In the CRS community, $\eta < 1$, making *Aphytis* the intraguild predator. Because omnivorous interactions such as IGP can take on any value in other communities, from only slight asymmetry to one-way consumption, we model IGP using this general form.

Combining the Poisson-distributed number of eggs laid with the biased lottery probability of emergence, we sum

over the numbers of species 1 (*Aphytis*) and species 2 (*Encarsia*) eggs to find

$$P(\text{species 1 emerges}) = \sum_{\substack{a,b=0 \\ a+b\neq0}}^{\infty} \frac{a}{a+\eta b} \frac{\mu_1^a \mu_2^b e^{-(\mu_1+\mu_2)}}{a!b!}, \quad (7)$$

$$P(\text{species 2 emerges}) = \sum_{\substack{a,b=0 \\ a+b\neq0}}^{\infty} \frac{\eta b}{a+\eta b} \frac{\mu_1^a \mu_2^b e^{-(\mu_1+\mu_2)}}{a!b!}, \quad (8)$$

where $\mu_1^a \mu_2^b e^{-(\mu_1+\mu_2)}/(a!b!)$ is the probability that the host contains $a$ species 1 eggs and $b$ species 2 eggs. To find the local dynamics for species $j$, we multiply the probability that species $j$ emerges by the density of hosts available for parasitism in that patch: $H_x' \exp(-\alpha H_x')$. Thus, denoting the density of species $j$ parasitoids emerging from a patch of type $x$ by $P_{jx}'(t)$,

$$P_{1x}'(t+1) = H_x' e^{-\alpha H_x'} \sum_{\substack{a,b=0 \\ a+b\neq0}}^{\infty} \frac{a}{a+\eta b} \frac{\mu_{1x}^a \mu_{2x}^b e^{-(\mu_{1x}+\mu_{2x})}}{a!b!}, \quad (9)$$

$$P_{2x}'(t+1) = H_x' e^{-\alpha H_x'} \sum_{\substack{a,b=0 \\ a+b\neq0}}^{\infty} \frac{\eta b}{a+\eta b} \frac{\mu_{1x}^a \mu_{2x}^b e^{-(\mu_{1x}+\mu_{2x})}}{a!b!}. \quad (10)$$

### Quantifying Coexistence

We use the standard mutual invasibility criterion for coexistence, which states that two species coexist if each species can recover from low density ("invade") in the presence of its competitor (the "resident"), which is not constrained to low density. We will denote invader quantities with subscript $i$ and resident quantities with subscript $r$. Choosing either species 1 or species 2 as resident, we let the invader density approach 0 and sum the series in equation (9) or (10) to find the number of resident parasitoids emerging from hosts at location $x$:

$$P_{rx}'(t+1) = H_x' e^{-\alpha H_x'}(1 - e^{-\mu_{rx}}). \quad (11)$$

This equation has a simple interpretation: the density of emerging parasitoids is equal to the density of hosts surviving competition, $H_x' e^{-\alpha H_x'}$, times the proportion of these hosts that are parasitized, $(1 - e^{-\mu_{rx}})$. We find the invader dynamics in the same manner. If species 1 is the invader, then we let $\overline{P_1}$ approach 0 in equation (9) to find

$$P_{i=1,x}'(t+1) = P_{ix}(t)a_i H_x' e^{-\alpha H_x'} e^{-\mu_{rx}} \sum_{b=0}^{\infty} \frac{1}{1+\eta b} \frac{\mu_{rx}^b}{b!}, \quad (12)$$

where $P_{ix}(t)$ is the density of ovipositing invaders in habitat $x$. As stated earlier, the local density of adults is equal to the average density times the affinity for habitat $x$: $P_{jx}(t) = E_{jx}\overline{P_j}(t)$. Similarly, if species 2 is the invader, then

$$P_{i=2,x}'(t+1) = P_{ix}(t)a_i H_x' e^{-\alpha H_x'} e^{-\mu_{rx}} \sum_{a=0}^{\infty} \frac{\eta}{a+\eta} \frac{\mu_{rx}^a}{a!}. \quad (13)$$

It will be helpful for our analysis to rewrite these equations in the form

$$P_{jx}'(t+1) = \lambda_{jx}(t)P_{jx}(t). \quad (14)$$

Here the density of species $j$ parasitoids emerging from a patch of type $x$ is expressed as a local rate of increase $\lambda_{jx}(t)$ times the local density of adults $P_{jx}(t)$. We will express $\lambda_{jx}(t)$ as a function of $C_{jx}(t)$, the competition experienced by species $j$ in habitat $x$. We define $C_{jx}(t)$ as the amount by which $\lambda_{jx}(t)$ is decreased by competition:

$$C_{jx}(t) \equiv \frac{\lim_{\overline{P_j}\to0} \lambda_{jx}(t)}{\lambda_{jx}(t)}. \quad (15)$$

The local rate of increase for species $j$ is then

$$\lambda_{jx} = \frac{H_0 a_j}{C_{jx}}, \quad (16)$$

where $H_0 = \ln F/(F\alpha)$ is the equilibrium density of the hosts after competition in the absence of parasitism (eq. [2]) and where we have suppressed time dependence ($t$) for clarity. The numerator is the rate of increase without competition while the denominator adjusts this to give the actual rate of increase. Expressions for resident competition $C_{rx}$ and invader competition $C_{ix}$ are given in table 1.

### Analytical Framework

To apply the analytical framework introduced by Chesson (2000*a*), we begin by writing the local rate of increase $\lambda_{jx}(t)$ in terms of species $j$'s environmental response $E_{jx}$ and its competition $C_{jx}(t)$. Where $E_{jx}$ is high, the environment is favorable and $\lambda_{jx}$ increases, while high competition $C_{jx}(t)$ causes $\lambda_{jx}$ to decrease. In this model, the environmental response is the affinity for habitat $x$, while competition is

**Table 1:** Expressions for resident and invader competition

| Competition type | Expression |
|---|---|
| Resident | $C_{rx} = \dfrac{H_0 \mu_{rx}}{H_x' e^{-\alpha H_x'}(1 - e^{-\mu_{rx}})}$ |
| Species 1 as invader | $C_{i=1,x} = \dfrac{H_0}{H_x' e^{-\alpha H_x'} e^{-\mu_{rx}} \sum_{b=0}^{\infty} \frac{1}{1+\eta b} \frac{\mu_{rx}^b}{b!}}$ |
| Species 2 as invader | $C_{i=2,x} = \dfrac{H_0}{H_x' e^{-\alpha H_x'} e^{-\mu_{rx}} \sum_{a=0}^{\infty} \frac{\eta}{a+\eta} \frac{\mu_{rx}^a}{a!}}$ |

due to resource exploitation and is equal to the growth rate in the absence of competitors divided by the growth rate in the presence of competitors.

Species coexistence is defined over some spatial extent, most sensibly the scale over which the community is effectively closed (Chesson 2000b). We call this scale the regional scale, and it is regional-scale rates of increase that determine coexistence. The regional-scale density is the spatial average density, $\overline{P}_j$, and the regional dynamics take the form $\overline{P}_j(t + 1) = \tilde{\lambda}_j(t)\overline{P}_j(t)$, where $\tilde{\lambda}_j$ is the average of the local growth rate over individuals from all patches in the system (Chesson 2000a). Thus, if the regional-scale finite rate of increase $\tilde{\lambda}_i$ is >1 for both species as invader, then each single species system is open to invasion by the other species, and the two species coexist.

The utility of this framework is that it allows the regional-scale rate of increase to be expressed as a sum of contributions from different classes of coexistence mechanisms, which allows us to weigh their relative importance. As explained by Chesson (2000a), the regional-scale rate of increase can be written as the sum of competitive differences and nonspatial coexistence mechanisms ($\tilde{\lambda}_i'$), the storage effect ($\Delta I$), relative nonlinearity ($\Delta N$), and growth-density covariance ($\Delta\kappa$). Mathematically,

$$\tilde{\lambda}_i = \tilde{\lambda}_i' + \Delta I - \Delta N + \Delta\kappa. \tag{17}$$

Let us discuss each term in turn.

*Competitive differences and nonspatial coexistence mechanisms* ($\tilde{\lambda}_i'$). This term consists of the difference in competitive abilities of the two species, averaged over all patches, and the effects of nonspatial coexistence mechanisms. In the absence of coexistence mechanisms, one species will exclude the other unless their average competitive abilities are precisely equal. Here, in the absence of intraguild predation, competitive differences arise from differences in the parasitoids' attack rates; the parasitoid with the higher attack rate is the better competitor. This competitive difference may be overcome by coexistence mechanisms. Many coexistence mechanisms, such as resource partitioning and trade-offs in the ability to gain different resources (MacArthur 1970; Tilman 1982), do not rely on spatial differentiation within a region. For example, it is possible for IGP to act alone as a coexistence mechanism in a uniform habitat as long as the poorer resource exploiter is also the intraguild predator (Holt and Polis 1997). Mathematically, IGP adds a positive contribution to $\tilde{\lambda}_i'$ for the intraguild predator, possibly making $\tilde{\lambda}_i' > 1$. However, coexistence will result only if $\tilde{\lambda}_i$ for the intraguild prey is not decreased below 1 by intraguild predation.

*Storage effect* ($\Delta I$). The storage effect arises from the interaction between the direct effects of environmental response and competition on growth. In this model, the environmental response is the habitat preference, and because it affects only the distribution of the parasitoids, the environmental response affects growth only indirectly, via competition. Because there is no direct effect on growth, there is no storage effect.

*Relative nonlinearity* ($\Delta N$). Relative nonlinearity arises when different species have different nonlinear responses to competition and competition varies in space. We can express competition as a function of one or more competitive factors. Such factors quantify different components of competition, which may affect different species in different ways. Here there are two competitive factors, labeled $F_1$ and $F_2$. The first competitive factor is postcompetition host density: $F_1 = H_x' e^{-\alpha H_x'}$. This density reflects the past effects of parasitoids on host density in a given patch. The second factor is the current competitive pressure of the resident parasitoid on hosts in a given patch (i.e., the local resident parasitoid density times its attack rate): $F_2 = a_r E_{rx}\overline{P}_r = \mu_{rx}$. When the local growth rate $\lambda_{jx}$ is a nonlinear function of the competitive factors, then variation in those factors may increase or decrease the regional-scale growth rate. Relative nonlinearity measures the degree to which the invader benefits from variability relative to the resident. (See "Summary of Basic Framework" in app. B for a quantitative definition.) When there is only habitat preference and no IGP, competition depends on the competitive factors in the same way for both species. Thus, neither species gains an advantage relative to the other by this mechanism, and $\Delta N = 0$. It is possible for $\Delta N$ to be nonzero, however, when IGP and habitat preference interact.

*Growth-density covariance* ($\Delta\kappa$). A species benefits when its population is concentrated in the areas most favorable to it (i.e., where its local growth rates are highest). Growth-density covariance measures the difference between the invader's and the resident's tendencies to concentrate their populations in this way. We quantify a species' tendency to aggregate in favorable areas by measuring the covariance between the local rate of increase and the relative population density, $\mathrm{Cov}(\lambda_j, \nu_j)$, where relative population density $\nu_{jx}$ equals the ratio of the local density of parasitoid $j$ to its average density: $\nu_{jx} = P_{jx}/\overline{P}_j$. (The covariance between two quantities $A$ and $B$ is equal to their correlation times the standard deviations of $A$ and $B$, so covariance accounts for both correlation and the magnitude of variation.) In this model, $\nu_{jx} = E_{jx}$. If species $j$'s population is concentrated in areas of high growth so that $\nu_j$ is large where $\lambda_j$ is large, then $\mathrm{Cov}(\lambda_j, \nu_j)$ will be large and positive. Growth-density covariance is defined mathematically as

$$\Delta\kappa = \mathrm{Cov}(\lambda_i, \nu_i) - q_{ir}\mathrm{Cov}(\lambda_r, \nu_r), \tag{18}$$

where $q_{ir}$ is a constant of comparison. This constant of comparison measures the relative sensitivity of the invader and resident growth rates to their common competitive factors. Because these common competitive factors mediate interactions between the species, this constant provides the appropriate basis for considering how changes in conditions for resident population growth translate into changes in conditions for invader population growth. (See "The Effect of $\eta$ on $q_{ir}$ and $\Delta\kappa$" in app. B for a more detailed discussion of $q_{ir}$.)

In this model, habitat preferences determine the distribution of parasitoids and therefore affect $\Delta\kappa$. In "Calculating $\tilde{\lambda}_i'$, $\Delta N$, and $\Delta\kappa$ in the Absence of IGP" in appendix B, we show that in the absence of IGP, all of the effects of habitat preference are summarized by $\Delta\kappa$.

When $\Delta I$, $\Delta\kappa$, or the nonspatial coexistence mechanism portion of $\tilde{\lambda}_i'$ is positive or $\Delta N$ is negative, the invader's regional-scale growth rate is increased. It is possible for a term to have the same sign for both species as invader, in which case it can promote coexistence by boosting the regional-scale growth rates of both species at low density. In the terminology of Chesson (2000*b*), this would be a predominantly stabilizing mechanism—one that, under an appropriate scaling, increases the regional growth rates of both species without changing their competitive difference. If the term increases the growth rate of only one species as invader, it can still promote coexistence by acting mostly as an equalizing mechanism (Chesson 2000*b*; one that decreases the competitive difference by changing the average fitness of each species by equal and opposite amounts) if it is positive for the inferior competitor and does not decrease $\tilde{\lambda}_i$ for the superior competitor below 1. Mechanisms can have both stabilizing and equalizing aspects to them. Appendix A shows how the stabilizing and equalizing components of a mechanism can be quantified and form the basis of the analysis of such components for our model.

## Results

### IGP, Habitat Preference, and Their Interaction

The solid lines in figure 1 show the coexistence regions produced by habitat preference alone. It is easiest to achieve coexistence if the two parasitoids have opposing habitat preferences but strict spatial segregation is not required; it is possible for the two to coexist with similar preferences (e.g., both prefer leaves) if the superior exploitative competitor (the one with the higher attack rate) has a strong preference while the inferior competitor's preference is weak. The superior competitor's strong preference leaves hosts in the less preferred area relatively untouched, so the less particular parasitoid is able to subsist on the leftovers of its competitor.
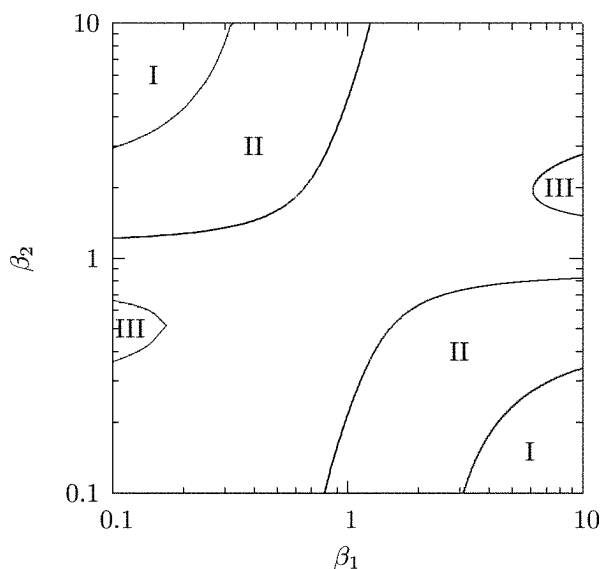


**Figure 1:** Coexistence regions with and without intraguild predation (IGP). The two species can coexist by habitat preference alone ($\eta = 1$) in the regions marked *I*. When IGP gives the inferior competitor a moderate advantage ($\eta = 0.25$), the coexistence regions expand to include the areas marked *II*. If IGP gives an even greater advantage to the inferior competitor ($\eta = 0.01$), the coexistence regions expands to include all but the areas marked *III*. Attack rate $a_1 = 3.5$ and $a_2 = 5.0$, host competition coefficient $\alpha = 1$, host fecundity $F = 5.0$, and the habitat is half leaves, half stems ($p_s = p_l = 0.5$).

Consistent with the results of other IGP models (Briggs 1993; Holt and Polis 1997; Borer 2002*a*; E. T. Borer, unpublished manuscript), IGP alone produces a very narrow ribbon of coexistence (fig. 2). Thus, IGP alone is unlikely to produce coexistence. On the other hand, adding IGP to a system with habitat preference can enlarge the coexistence regions if IGP gives a moderate advantage to the inferior competitor or can diminish the coexistence regions if it either confers an excessive advantage or favors the superior competitor.

The result when both mechanisms are present is not a simple sum of the effects of each singly. We can see the interaction between habitat preference and IGP when we plot $\tilde{\lambda}_i$ with and without IGP, as in figure 3. The curve produced by habitat preference changes shape when IGP is added instead of simply shifting up or down, as it would if the effects were additive. This interaction has an intuitive explanation. When the resident has a strong habitat preference, then there will be many residents in the preferred habitat. Almost all hosts will have been parasitized at least once by the resident, and IGP favoring the invader can significantly increase the number of emerging invaders. Stated another way, interspecific competition will be high for the invader in the resident's preferred habitat, and IGP
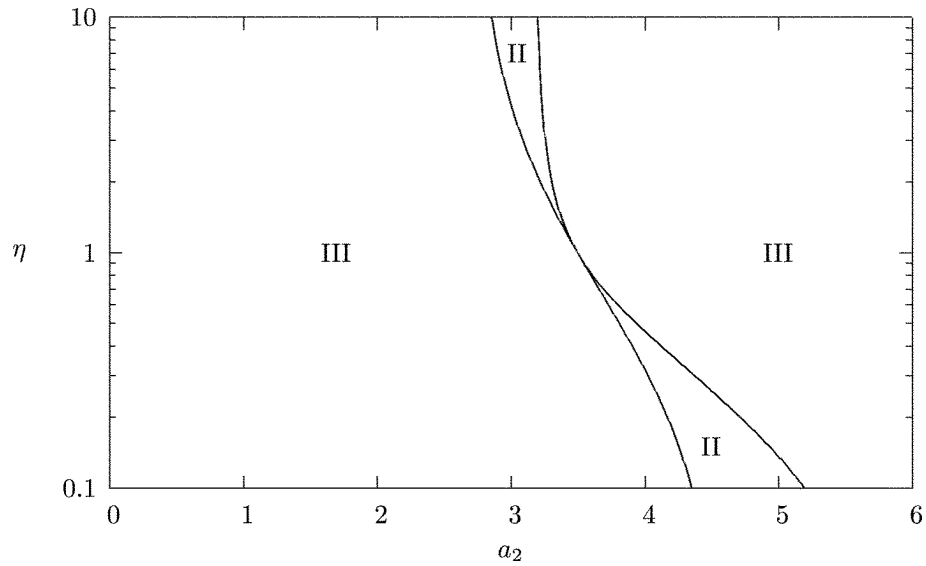
**Figure 2:** Coexistence regions in the presence of intraguild predation (IGP) only. Species coexist in the regions marked *II* and cannot coexist in the regions marked *III*. IGP alone provides only a very narrow coexistence region. $\beta_1 = \beta_2 = 1.0$ (no habitat preference). All other parameters are as in figure 1.

favoring the invader can reduce that competition substantially. In the resident's less preferred habitat, on the other hand, there will be few residents. In many cases, a host will be parasitized only by the invader, so IGP is of no advantage. Here invader competition is small, and IGP lowers $C_i$ only a little. The stronger the habitat preference,
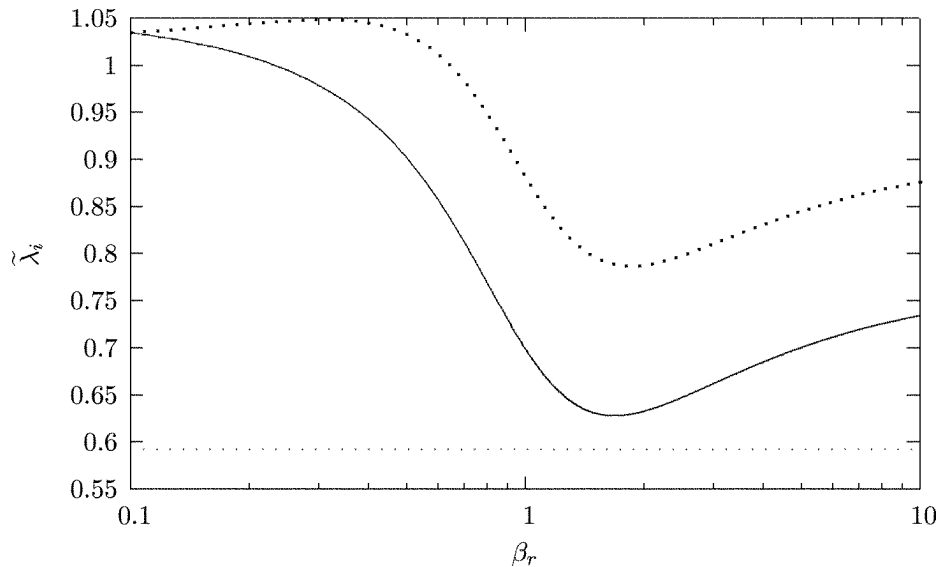


**Figure 3:** Regional-scale growth rates for species 1 as invader. The solid line shows $\tilde{\lambda}_i$ when only habitat preference is present, the light dotted line indicates $\tilde{\lambda}_i$ when only intraguild predation (IGP) is present (IGP does not depend on $\beta$, so this is a straight line), and the heavy dotted line shows $\tilde{\lambda}_i$ when both IGP and habitat preference are present. To make it easier to compare their shapes, this line has been shifted downward to coincide with the habitat preference–only line at $\beta_r = 0.1$. When IGP is present, $\eta = 0.2$. Invader habitat preference $\beta_i = 5.0$. All other parameters are as in figure 1.
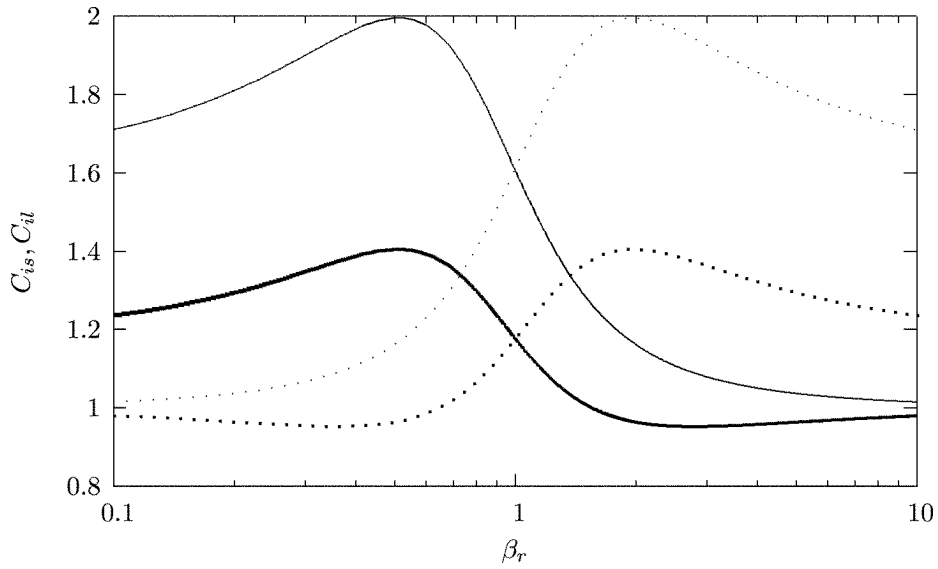
**Figure 4:** Invader competition with and without intraguild predation (IGP) for species 1 as invader. The light solid line and light dotted line show $C_{is}$ and $C_{il}$ without IGP, while the heavy solid line and heavy dotted line show $C_{is}$ and $C_{il}$ with IGP that favors the invader ($\eta = 0.2$). Invader habitat preference $\beta_i$ is irrelevant; $a_1 = 3.5$, $a_2 = 5.0$. All other parameters are as in figure 1.

the greater the disparity between the effects of IGP on $C_{is}$ and $C_{il}$.

We can see this interaction in figure 4, which shows the intensity of competition experienced by the invader on stems and leaves as a function of resident habitat preference. As $\beta_r$ becomes small so that the resident has a strong preference for stems, $C_{is}$ becomes large and is substantially reduced by IGP, while $C_{il}$ is small and is reduced
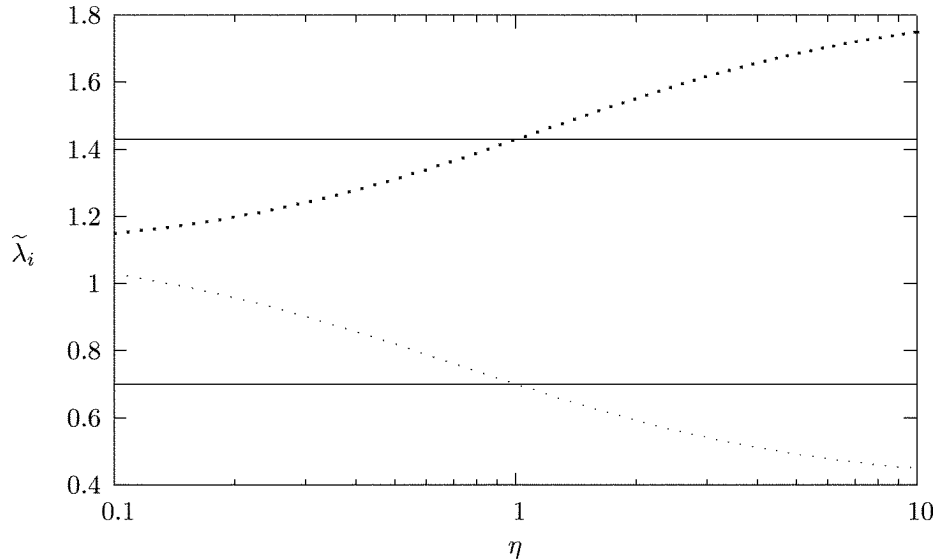


**Figure 5:** Invader regional-scale growth rates in the absence of habitat preference. The two solid lines show the growth rates of both species as invader in the absence of both habitat preference and intraguild predation (IGP), while the dotted lines show their growth rates when IGP is added. The light dotted line shows $\tilde{\lambda}_i$ for species 1, which is the intraguild predator when $\eta < 1$ and the intraguild prey when $\eta > 1$. The heavy dotted line shows $\tilde{\lambda}_i$ for species 2, which is the intraguild predator when $\eta > 1$ and the intraguild prey when $\eta < 1$. All other parameters are as in figure 1.
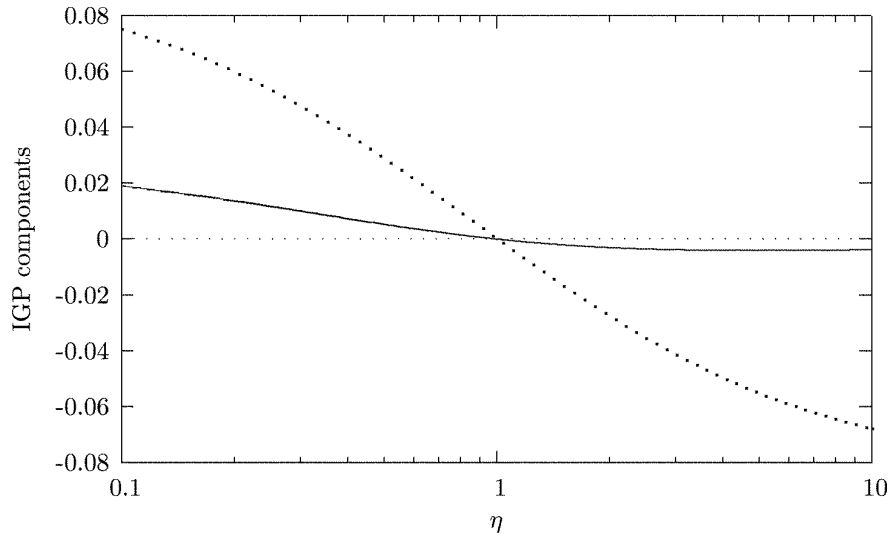
**Figure 6:** Stabilizing and equalizing components of intraguild predation (IGP) in the absence of habitat preference. Parameters are as in figure 1. The solid line shows the stabilizing component of IGP, while the heavy dotted line shows the equalizing component. (See app. A for an explanation of how to calculate these components.) A light dotted line at 0 has been added as an aid to the eye. IGP acting in the absence of habitat preference is primarily an equalizing mechanism.

only slightly. Similarly, as $\beta_r$ becomes large so that the resident has a strong preference for leaves, $C_{il}$ is large and sensitive to IGP, while $C_{is}$ is small and is little changed by the addition of IGP. We examine the implications of this interaction in the following section.

### Analysis Using $\tilde{\lambda}'_i$, $\Delta N$, and $\Delta \kappa$

The analytical framework described in "Analytical Framework" gives us a different way to probe the effects of habitat preference, IGP, and their interaction. As shown
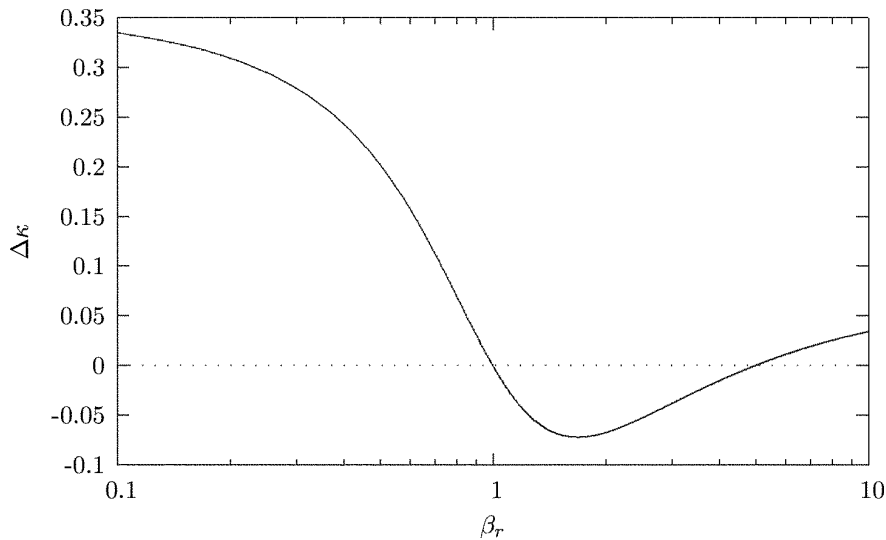


**Figure 7:** Growth-density covariance ($\Delta \kappa$) with habitat preference alone (no intraguild predation). The solid line shows $\Delta \kappa$ in the presence of habitat preference alone ($\eta = 1$). The invader prefers leaves ($\beta_i = \beta_1 = 5.0$). All other parameters are as in figure 1.
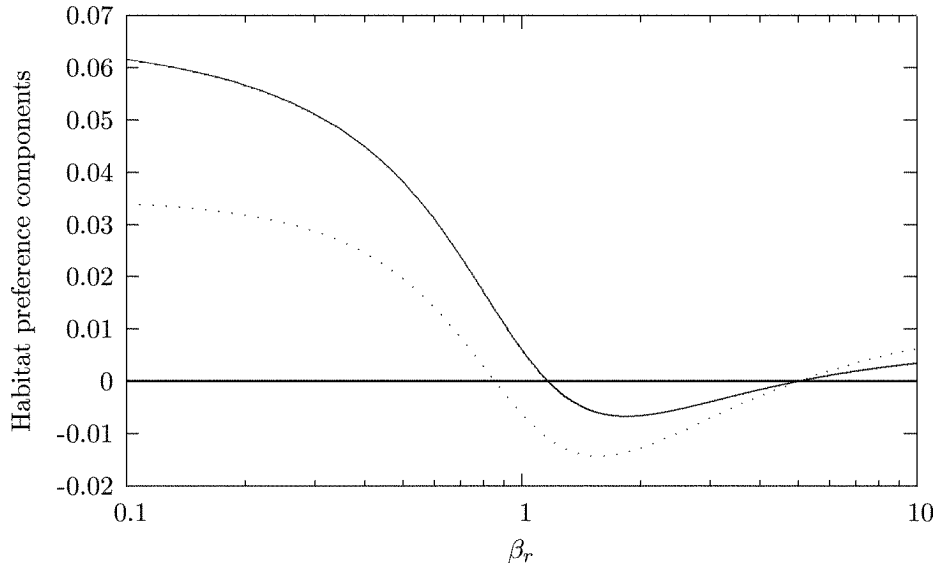
**Figure 8:** Stabilizing and equalizing components of habitat preference in the absence of intraguild predation (IGP). Parameters are as in figure 1. The solid line shows the stabilizing component of habitat preference, while the dotted line shows the equalizing component. (See app. A for an explanation of how to calculate these components.) We see that in the absence of IGP, habitat preference is primarily a stabilizing mechanism for most levels of resident habitat preference; however, when both resident and invader prefer the same habitat and the invader persists by being less of a specialist than the resident ($\beta_r > 5$ in this figure), habitat preference is dominated by its equalizing component.

in "Calculating $\tilde{\lambda}'_i$, $\Delta N$, and $\Delta \kappa$ in the Absence of IGP," the effects of IGP alone are given by $\tilde{\lambda}'_i$, the effects of habitat preference alone by $\Delta \kappa$, and their interaction by $\Delta N$ and an additional contribution to $\Delta \kappa$. As we shall show below, the effects of habitat preference and IGP are sometimes subadditive and sometimes superadditive; the whole may be less than or greater than the sum of its parts.

When there is neither IGP nor habitat preference, the invader's regional-scale growth rate is given by

$$\tilde{\lambda}_i = \tilde{\lambda}'_i = \frac{a_i}{a_r} \qquad (19)$$

("Calculating $\tilde{\lambda}'_i$, $\Delta N$, and $\Delta \kappa$ in the Absence of IGP"). When the species with the higher attack rate is the invader, $\tilde{\lambda}_i > 1$, and the invader increases in number; when the species with the lower attack rate is the invader, $\tilde{\lambda}_i < 1$, and the invader decreases in number. No coexistence is possible unless the two attack rates are precisely equal.

Introducing IGP adds a contribution to invader growth, positive for the intraguild predator and negative for the intraguild prey. IGP is a nonspatial coexistence mechanism, so this contribution is added to $\tilde{\lambda}'_i$:

$$\tilde{\lambda}_i = \tilde{\lambda}'_i = \frac{a_i}{a_r} + \text{IGP contribution.} \qquad (20)$$

Figure 5 shows the regional-scale rate of increase ($\tilde{\lambda}_i$) of both species as invader as a function of the strength of IGP ($\eta$).

Because IGP adds to the growth rate of one species at the expense of the other, it is primarily an equalizing mechanism (see fig. 6). It can even out competitive differences caused by unequal attack rates and in some cases adds more to one than it subtracts from another, giving a slight stabilizing effect. But too much of a drift in one direction or the other will destroy the balance, and so the region of coexistence provided by IGP alone is necessarily narrow.

**Table 2:** The effects of habitat preference in the absence of IGP

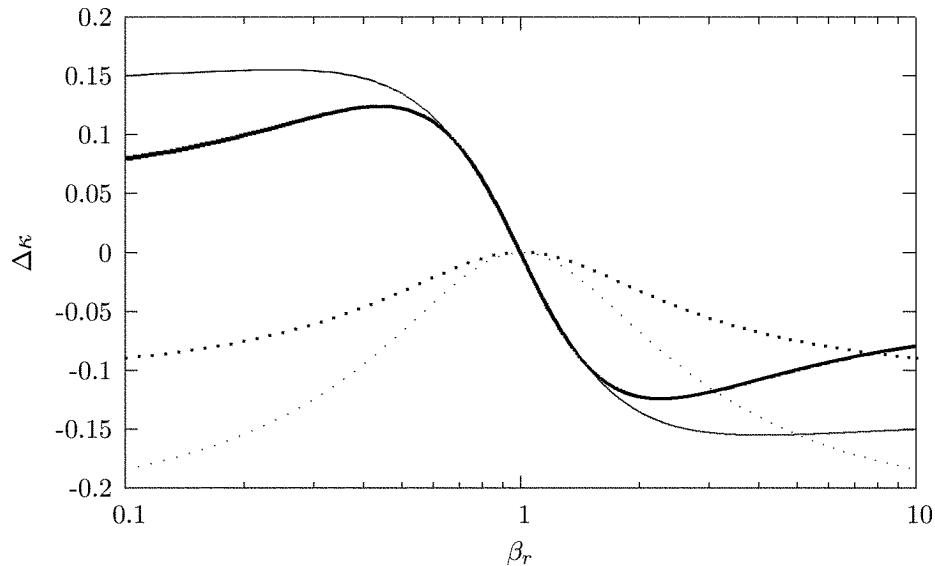| Resident and invader preference | $\Delta \kappa$ | Regional invader growth $\tilde{\lambda}_i$ |
|---|---|---|
| Different habitats | Positive | Increased |
| Same habitat, invader has weaker preference | Positive | Increased |
| Same habitat, invader has stronger preference | Negative | Decreased |

**Figure 9:** Components of $\Delta\kappa$ with and without intraguild predation (IGP). The light and heavy solid lines show Cov$(\lambda_i, \nu_i)$ without IGP and with IGP favoring the invader ($\eta = 1$ and $\eta = 0.2$), respectively. The light and heavy dotted lines show $q_{ir}$ Cov$(\lambda_r, \nu_r)$ with $\eta = 1$ and $\eta = 0.2$, respectively. The invader prefers leaves ($\beta_i = \beta_1 = 5.0$). All other parameters are as in figure 1.

When there is only habitat preference and no IGP, the invader's regional-scale growth rate is given by

$$\tilde{\lambda}_i = \frac{a_i}{a_r} + \Delta\kappa, \qquad (21)$$

so all of the effects of habitat preference are contained in $\Delta\kappa$, the relative tendency of the invader to be aggregated in areas where its growth rate ($\lambda_i$) is high ("Calculating $\tilde{\lambda}_i$, $\Delta N$, and $\Delta\kappa$ in the Absence of IGP"). Figure 7 shows how $\Delta\kappa$ changes as the resident habitat preference changes, and figure 8 partitions this into stabilizing and equalizing components. If both species prefer the same habitat, then $\Delta\kappa$ will be positive for the species with the weaker preference and negative for the other, so habitat preference acts primarily as an equalizing mechanism, just as IGP does. However, if the species prefer different habitats, then $\Delta\kappa$ will be positive for both species as invader and will act primarily as a stabilizing mechanism, promoting coexistence more broadly. This information is summarized in table 2. In figure 7, the invader prefers leaves ($\beta_i = 5$),

and $\Delta\kappa$ is negative when the resident has a weaker preference for leaves ($\beta_r$ between 1 and 5) but is positive when the resident has a stronger preference for leaves or when it prefers stems.

Biologically, this happens because the distribution of the resident is determined by the resident's habitat preference ($\beta_r$), not by the density of hosts, and so the stronger the resident preference, the more host density will be suppressed in the preferred habitat and the more the resident will be concentrated in areas of lower resident growth (Cov$[\lambda_r, \nu_r]$ will be more negative). If the invader prefers the other habitat, then it will be concentrated where host density has been less suppressed, in areas of higher invader growth (Cov$[\lambda_i, \nu_i]$ will be positive). The invader therefore tracks its resource better than the resident and gains an advantage, summarized by a positive value for $\Delta\kappa$. If, on the other hand, the invader prefers the same habitat as the resident, then it too will be concentrated in areas of lower growth. Nonetheless, if it has a weaker preference than the resident, then it will not be concentrated quite so strongly and will again gain an advantage ($\Delta\kappa$ positive).

**Table 3:** The effects of adding IGP to habitat preference

| Invader | Cov($\lambda_i, \nu_i$) | $q_{ir}$ | $\Delta\kappa$ | IGP + habitat preference |
|---|---|---|---|---|
| Intraguild predator | Decreases | Decreases | Decreases | Subadditive |
| Intraguild prey | Increases | Increases | Increases | Superadditive |

Note: Here we assume that the invader and resident prefer different habitats.
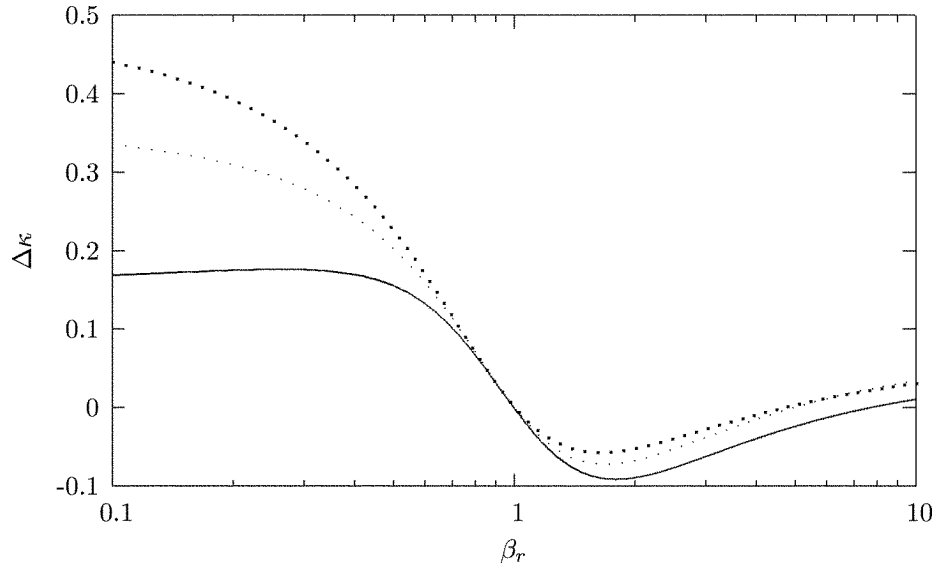
**Figure 10:** Growth-density covariance ($\Delta\kappa$) vs. resident habitat preference ($\beta_r$) with and without intraguild predation (IGP). The light dotted line shows $\Delta\kappa$ in the absence of IGP (only habitat preference). The solid line shows $\Delta\kappa$ when the invader is the intraguild predator ($\eta = 0.2$), while the heavy dotted line shows $\Delta\kappa$ when the invader is the intraguild prey ($\eta = 5.0$). The invader prefers leaves ($\beta_i = \beta_1 = 5$). All other parameters are as in figure 1.

When habitat preference and IGP are both present, as in the CRS community, their interaction causes $\Delta N$ to be nonzero and adds an additional contribution to $\Delta\kappa$. These effects are in addition to the effects that IGP and habitat preference provide in isolation so that when both mechanisms are present, $\tilde{\lambda}'_i$, $\Delta N$, and $\Delta\kappa$ are all nonzero. The magnitude of $\Delta N$ is small, however, so the interaction between IGP and habitat preference is expressed mainly by changes in $\Delta\kappa$. (While growth can be a strongly nonlinear function of competition in this model, invader growth and resident growth are relatively similar functions of competition; they are not strongly nonlinear with respect to each other.)

Figure 10 shows $\Delta\kappa$ with and without IGP, so the differences between the lines show what the interaction between habitat preference and IGP contributes to $\Delta\kappa$. The way to understand the interaction is to consider the components of $\Delta\kappa$: $\mathrm{Cov}\,(\lambda_i, \nu_i)$ and $q_{ir}\,\mathrm{Cov}\,(\lambda_r, \nu_r)$. These are both plotted in figure 9, with and without IGP.

IGP does not affect the resident's growth rate ($\lambda_r$) and so has no effect on $\mathrm{Cov}\,(\lambda_r, \nu_r)$. However, it does change the way invader growth depends on the competitive factors and thus changes $q_{ir}$, which relates the relative sensitivities of the resident and invader to these factors. As explained in "The Effect of $\eta$ on $q_{ir}$ and $\Delta\kappa$," $q_{ir}$ decreases when the invader becomes an intraguild predator. Because the resident locally depresses host density when it is aggregated, $\mathrm{Cov}\,(\lambda_r, \nu_r)$ is negative, and so this makes $q_{ir}\,\mathrm{Cov}\,(\lambda_r, \nu_r)$

increase (i.e., become less negative/more positive). When the invader becomes an intraguild predator, $\mathrm{Cov}\,(\lambda_i, \nu_i)$ decreases if the resident and invader prefer different habitats ($\beta_r < 1$ in fig. 9) and increases if they prefer the same habitat ($\beta_r > 1$ in fig. 9). If the invader becomes an intraguild prey instead, the effects of the components of $\Delta\kappa$ are reversed. These effects are summarized in table 3 and are explained in fuller detail in "The Effect of $\eta$ on $q_{ir}$ and $\Delta\kappa$."

Putting this information together, we find that when the invader and resident prefer different habitats, IGP affects both components of $\Delta\kappa$ similarly so that when IGP favors the invader, the invader's relative tendency to be aggregated in favorable areas ($\Delta\kappa$) decreases, and when IGP favors the resident, $\Delta\kappa$ increases. Stated another way, when the two parasitoids prefer different habitats, the interaction of IGP and habitat preference adds a negative contribution to the regional-scale growth rate ($\tilde{\lambda}_i$) of the intraguild predator as invader and adds a positive contribution to the regional-scale growth rate of the intraguild prey as invader; the species that benefits from IGP benefits less than it otherwise would from habitat preference, while the species that is hurt by IGP benefits more from habitat preference. The contributions of IGP and habitat preference are thus subadditive for the intraguild predator and superadditive for the intraguild prey. We see this in figure 10, in which the invader prefers leaf habitat ($\beta_i = 5.0$). When the resident prefers stems ($\beta_r < 1$), $\Delta\kappa$ in the pres-
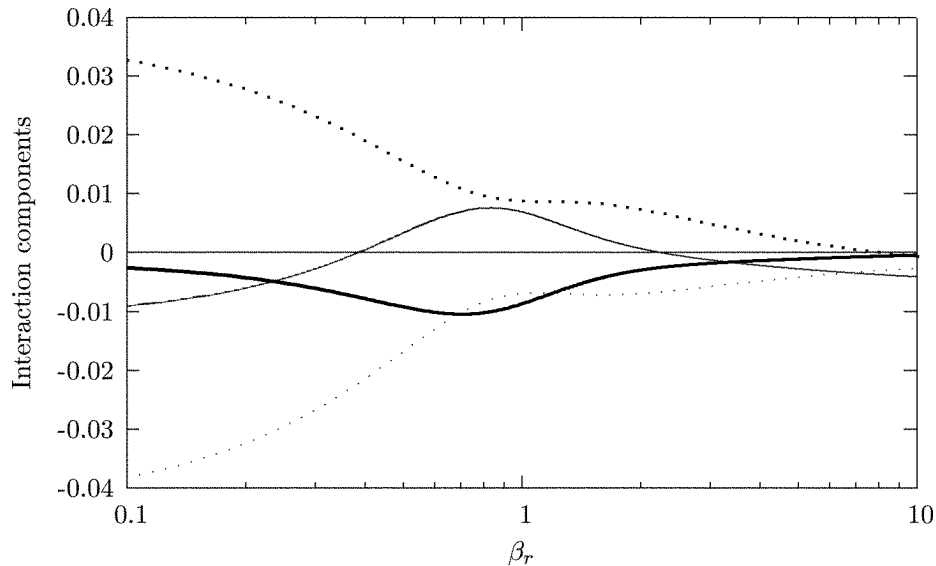
**Figure 11:** Stabilizing and equalizing components of the interaction between habitat preference and intraguild predation (IGP). Parameters are as in figure 1. For $\eta = 0.2$ (species 1, acting as the invader, is the intraguild predator), the light solid line shows the stabilizing component of the interaction between habitat preference and IGP, while the light dotted line shows the equalizing component. For $\eta = 5$ (species 1, acting as the invader, is the intraguild prey), the heavy solid line shows the stabilizing component, and the heavy dotted line shows the equalizing component.

ence of IGP decreases for the intraguild predator as invader (*solid line*) and increases for the intraguild prey as invader (*heavy dotted line*).

The negative interaction that occurs when the invader is the intraguild predator and the positive interaction when it is the intraguild prey come about largely as an equalizing mechanism. The advantage conferred upon the invader by IGP is partially offset by the interaction of habitat preference and IGP. There is also a weaker stabilizing component that is antistabilizing for strong resident habitat preference ($\beta_r$ near 0.1) and stabilizing for weak resident habitat preference ($\beta_r$ near 1). Figure 11 shows the partitioning of the interaction term into stabilizing and equalizing components.

In the contrasting scenario when the two species prefer the same habitat, IGP changes the components of $\Delta\kappa$ in opposing directions, and the interaction between IGP and habitat preference may cause $\Delta\kappa$ to increase or decrease. We see this complicated situation in figure 10, in which the invader prefers leaf habitat ($\beta_i = 5.0$). When the resident also prefers leaves ($\beta_r > 1$), the addition of IGP causes $\Delta\kappa$ to increase or decrease depending on the value of $\beta_r$.

### Discussion

In summary, we find that IGP acts primarily as an equalizing mechanism in this model, adding to the growth rate of one species at the expense of another. If IGP alone

enables coexistence, then it does so by evening out the growth rates of the two species so that both lie just above 1. This is a delicate balance, however, and so the coexistence region generated by IGP alone is always small. This is consistent with the findings of IGP models regardless of formulation (Briggs 1993; Holt and Polis 1997; Borer 2002*a*; E. T. Borer, unpublished manuscript).

Habitat preference, on the other hand, is primarily stabilizing if the two species prefer different substrates, boosting the low-density growth rates of both species. (If both species prefer the same habitat, then habitat preference acts mostly as an equalizing mechanism, favoring the species with the weaker preference at the expense of the other.) Because stabilizing mechanisms increase the growth rates of both species as invaders, they tend to result in much broader coexistence regions and are more likely to contribute to the coexistence of real species.

Perhaps most interestingly, the effects of habitat preference and IGP are not independent but instead interact. This arises naturally from our model rather than being included explicitly. When the two parasitoids prefer different habitats, the intraguild predator benefits less from habitat preference as an invader than it would in the absence of IGP, while the intraguild prey benefits more from habitat preference as invader. The net effect is that the habitat preference promotes coexistence more strongly if IGP gives a moderate advantage to the inferior competitor. When the two parasitoids prefer the same habitat, the

interaction of habitat preference with IGP is more complex and no general statements can be made.

Although our primary goal here was a general exploration of the interaction of two coexistence mechanisms, it was motivated by a real biological system. Even in the absence of a full analysis of this model using system-specific parameter values, the general model results presented here can provide us with insights into parasitoid coexistence in the red scale system. The habitat preferences of both *Aphytis* and *Encarsia* are relatively weak (Borer et al. 2004), so habitat preference alone is able to maintain coexistence only when the two species have similar attack rates. Attack rates, though difficult to measure exactly, are likely to be quite different, with *Encarsia* attacking scale more rapidly than *Aphytis* (Borer 2002*a*), suggesting that habitat preference alone may be insufficient to maintain coexistence. In addition, the narrow coexistence region generated by IGP alone in this model suggests that IGP is unlikely to be the sole mechanism enabling coexistence in this system. Because the competing parasitoids prefer different habitats, however, the interaction of habitat preference and IGP will enlarge the coexistence region, suggesting that the combination of habitat preference and IGP may facilitate coexistence of *Aphytis* and *Encarsia* on red scale.

This argument depends in part on our finding that the coexistence region produced by IGP is narrow while the coexistence region produced by habitat preference is relatively broad. We note that similar results were found with more biologically realistic, stage-structured models (Borer 2002*a*; E. T. Borer, unpublished manuscript). Again, we believe that this is because, as a trade-off, IGP inevitably acts largely as an equalizing mechanism, whereas habitat preference is mostly a stabilizing mechanism when the two parasitoids prefer different habitats. It is important to note, however, that although habitat preference enables coexistence over a broader range of parameters than IGP does, the maximum potential contributions of IGP and habitat preference to the invaders' regional growth rate ($\tilde{\lambda}_i$) are roughly equal, as can be seen by comparing figures 5 and 7.

We advocate measuring the effects of different coexistence mechanisms on the invader's regional growth rate separately and in combination as a way of quantifying their contributions to coexistence. The partitioning scheme presented by Chesson (2000*a*) provides one way to do this. Of course, this framework provides its own classification of coexistence mechanisms ($\Delta I$, $\Delta N$, etc.). For this model, these categories are in one-to-one correspondence with the biological mechanisms (IGP and $\tilde{\lambda}_i'$, habitat preference and $\Delta\kappa$), but in general this need not be so. Nonetheless, applying this partitioning scheme can still be useful because it offers a different way of categorizing contributions to coexistence and allows one to identify biological mechanisms that are promoting coexistence in the same way (different forms of $\Delta I$, for example).

Our model is similar to those of May and Hassell (1981) and Hogarth and Diamond (1984) in that parasitoid density is determined by factors other than host density. Klopfer and Ives (1997) term this "density-independent aggregation" and note that density-independent aggregation promotes coexistence more effectively than does density-dependent aggregation, in which both species aggregate in areas of high host density to different degrees. In all cases, what allows coexistence is the concentration of the invader in areas of high growth (i.e., growth-density covariance). We note in passing Amaresekare's (2000) study of coexisting harlequin bug parasitoids, a system in which both spatial mechanisms and IGP are also possible coexistence mechanisms. Finding no evidence of a competition-colonization trade-off, she states that "these results strongly suggest that parasitoid coexistence occurs via local interactions rather than spatial processes" (Amaresekare 2000, p. 1286). We have shown that habitat preference, a different form of spatial process, may promote coexistence over a broader range of conditions than IGP.

Finally, we emphasize that coexistence in many natural systems is likely to be sustained by multiple mechanisms, many of which will interact. If we consider mechanisms only one at a time, we will miss these interactions, which can substantially alter the net result.

## APPENDIX A

### Stabilizing and Equalizing Components of Mechanisms

Invader growth rates in two-species systems can often be put in the form

$$\frac{\tilde{\lambda}_i - 1}{d_i} = \mu_i - \mu_r + A, \tag{A1}$$

where $d_i$ is a scaling factor, $\mu_i$ and $\mu_r$ represent average fitness measures for each of the two species in the absence of specific coexistence mechanisms, and $A$ is a term representing the effect of these particular coexistence mechanisms (Chesson 2000b, 2003). Let us choose $d_i$ such that the fitness difference terms $\mu_i - \mu_r$ sum to 0; that is, $(\tilde{\lambda}_i - 1)/d_i$ sums to 0 over both species as invader in the absence of the specific coexistence mechanisms in question. This allows us to rewrite $\mu_i - \mu_r$ as

$$\mu_{i=1} - \mu_{r=2} = \frac{1}{2}\left(\frac{\tilde{\lambda}_{i=1} - 1}{d_1} - \frac{\tilde{\lambda}_{i=2} - 1}{d_2}\right) \quad (A2)$$

for species 1 as invader (similarly for species 2) and to rewrite $A$ as

$$A = \frac{1}{2}\left(\frac{\tilde{\lambda}_{i=1} - 1}{d_1} + \frac{\tilde{\lambda}_{i=2} - 1}{d_2}\right). \quad (A3)$$

Here, $a_j$ is a natural choice for $d_j$ and gives $\mu_i - \mu_r$ equal to $1/a_i - 1/a_r = (\tilde{\lambda}_i - 1)/a_i$ in the absence of IGP and habitat selection.

The equalizing and stabilizing components of a new mechanism are, respectively, the changes that occur in each of the quantities (A2) and (A3). For example, when habitat preference is introduced, $\mu_{i=1} - \mu_{r=2}$ becomes

$$\frac{1}{a_2} - \frac{1}{a_1} + \frac{1}{2}\left(\frac{\Delta\kappa_{i=1}}{a_1} - \frac{\Delta\kappa_{i=2}}{a_2}\right),$$

and $A$ becomes

$$\frac{1}{2}\left(\frac{\Delta\kappa_{i=1}}{a_1} + \frac{\Delta\kappa_{i=2}}{a_2}\right).$$

The equalizing component of habitat preference is thus

$$\frac{1}{2}\left(\frac{\Delta\kappa_{i=1}}{a_1} - \frac{\Delta\kappa_{i=2}}{a_2}\right),$$

and the stabilizing component is

$$\frac{1}{2}\left(\frac{\Delta\kappa_{i=1}}{a_1} + \frac{\Delta\kappa_{i=2}}{a_2}\right).$$

A purely equalizing mechanism reduces average fitness differences so that $(\tilde{\lambda}_{i=1} - 1)/d_1 - (\tilde{\lambda}_{i=2} - 1)/d_2$ decreases in absolute magnitude, with no change in the sum $(\tilde{\lambda}_{i=1} - 1)/d_1 + (\tilde{\lambda}_{i=2} - 1)/d_2$. A purely stabilizing mecha-

nism increases the sum of these scaled invader rates of increase without changing the difference. If a stabilizing mechanism increases $A$ enough, then both invader-scaled rates of increase become positive, implying species coexistence. Stabilizing and equalizing mechanisms can also work in concert. If a stabilizing mechanism has given positive $A$ values to each species but these are not large enough for both scaled invader rates of increase to be positive, a purely equalizing mechanism can lead to coexistence by reducing the fitness difference that needs to be overcome by the stabilizing mechanism.

Most mechanisms have both stabilizing and equalizing properties (or their opposites) in most settings. The exceptions are special cases often chosen with various kinds of strict symmetry rarely found in nature. For example, with the attack rates $a_j$ the same for each species, and opposite but symmetric habitat preferences, $\Delta\kappa$ is purely stabilizing here, leaving fitness differences at 0 but increasing the sum of the scaled growth rates, leading to stable coexistence. Similarly, any mechanism here that acted directly on the $a_j$ in the absence of IGP or habitat preference could only be equalizing or its opposite. Most mechanisms, however, affect both the difference of the scaled growth rates and their sum and therefore have both equalizing and stabilizing components. In this context, we note that IGP is mostly equalizing when the $\eta$ value is higher for the species with the lower $a_i$, but habitat preference is mostly stabilizing, that is, has a stronger stabilizing than equalizing component.

## APPENDIX B

### Mathematics

#### *Summary of the Basic Framework*

In this appendix we present a summary of the basic framework used to partition the regional finite growth rate ($\tilde{\lambda}$) into nonspatial mechanisms of coexistence ($\tilde{\lambda}'$), the storage effect ($\Delta I$), nonlinear competition ($\Delta N$), and growth-density covariance ($\Delta\kappa$). For full details, see Chesson (2000a).

Suppose that the local finite rate of increase is given by

$$\lambda_j(x, t) = G_j[E_j(x), C_j(x, t)]. \quad (B1)$$

We put this into a standard form by choosing $E_j^*$ and $C_j^*$ such that

$$G_j(E_j^*, C_j^*) = 1 \quad (B2)$$

and by defining

$$\mathcal{E}_j(x) = G_j[E_j(x), C_j^*] - 1, \tag{B3}$$

$$\mathcal{C}_j(x, t) = 1 - G_j[E_j^*, C_j(x, t)]. \tag{B4}$$

Ideally, we choose $E_j^*$ and $C_j^*$ such that $\mathcal{E}_j = O(\sigma)$ and $\langle \mathcal{E}_j \rangle = O(\sigma^2)$, where $\sigma$ is a small parameter representing the magnitude of the variance in the environmental responses[4]. When $E_j = E_j^*$, $\mathcal{E}_j = 0$, so these requirements mean that $E_j^*$ should be a "typical" value of $E_j$ so that $\mathcal{E}_j$ fluctuates about a value close to 0 and does not vary too wildly. The assumptions in Chesson's (2000*a*) appendix III then guarantee that $\mathcal{C}_j = O(\sigma)$ and $\langle \mathcal{C}_j \rangle = O(\sigma^2)$. Recasting the problem in terms of the standardized variables $\mathcal{E}_j$ and $\mathcal{C}_j$ then allows us to make the quadratic approximation

$$\lambda_j - 1 \approx \mathcal{E}_j - \mathcal{C}_j + \gamma_j \mathcal{E}_j \mathcal{C}_j, \tag{B5}$$

$$\gamma_j = \left. \frac{\partial^2 \lambda_j}{\partial \mathcal{E}_j \partial \mathcal{C}_j} \right|_{\mathcal{E}_j = \mathcal{C}_j = 0}, \tag{B6}$$

while still retaining much of the original nonlinearity of the problem. (Many models, including the one analyzed in this article, obey eq. [B5] exactly. In such a case it is less critical to ensure that $\mathcal{E}_j = O(\sigma)$ and $\langle \mathcal{E}_j \rangle = O(\sigma^2)$.) We can then write

$$\tilde{\lambda}_i \approx 1 + \Delta E - \Delta C + \Delta I + \Delta \kappa, \tag{B7}$$

where

$$\Delta E = \langle \mathcal{E}_i \rangle - q_{ir} \langle \mathcal{E}_r \rangle, \tag{B8}$$

$$\Delta C = \langle \mathcal{C}_i^{-i} \rangle - q_{ir} \langle \mathcal{C}_r^{-i} \rangle, \tag{B9}$$

$$\Delta I = \gamma_i \langle \mathcal{E}_i \mathcal{C}_i^{-i} \rangle - q_{ir} \gamma_r \langle \mathcal{E}_r \mathcal{C}_r^{-i} \rangle, \tag{B10}$$

$$\Delta \kappa = \mathrm{Cov}\,(\lambda_i, \nu_i) - q_{ir} \mathrm{Cov}\,(\lambda_r, \nu_r). \tag{B11}$$

The quantity $q_{ir}$ is a constant allowing appropriate comparison of invader and resident growth rate terms and is defined below. The covariances are evaluated at 0 lag, and the superscript $-i$ designates a quantity calculated with invader density set to 0. The angular brackets denote a spatial average, just as an overbar does.

It is helpful to consider the nonlinear portion of $\Delta C$ separately because it is partly $\lambda$'s nonlinear dependence on $C$ that shifts $\tilde{\lambda}_i$ away from the value it would take in a uniform environment. In the following paragraph, therefore, we Taylor expand $\Delta C$, lumping the constant terms with $1 + \Delta E$ to form $\tilde{\lambda}_i'$, choosing $q_{ir}$ such that the linear

terms vanish and retaining the nonlinear portion to form $\Delta N$ so that

$$\tilde{\lambda}_i = \tilde{\lambda}_i' - \Delta N + \Delta I + \Delta \kappa. \tag{B12}$$

Suppose that competition is determined by a collection of competitive factors $F_1$, $F_2$, ..., so that

$$\mathcal{C}_j^{-i} = \phi_j(\mathbf{F}), \tag{B13}$$

where $\mathbf{F}$ is a vector with components $F_1$, $F_2$, .... (For example, in this article, we have taken our competitive factors to be postcompetition host density $[H_x' e^{-\alpha H_x'}]$ and the local resident parasitoid density times its attack rate $[a_r E_{rx} \overline{P}_r = \mu_{rx}]$.) We expand about $\mathbf{F} = \mathbf{F}^*$, where $\mathbf{F}^*$ is the value taken by $\mathbf{F}$ when $E_{rs} = E_{rl} = E_r^*$. Note that when $\mathbf{F} = \mathbf{F}^*$, $E_{jx} = E_r^*$ and $C_{jx} = C_r^*$, so $\phi_j(\mathbf{F}^*) = 1 - G_j(E_r^*, C_r^*)$;

$$\mathcal{C}_j = \phi_j(\mathbf{F}) = \phi_j(\mathbf{F}^*) + \nabla\phi_j(\mathbf{F}^*) \cdot (\mathbf{F} - \mathbf{F}^*)$$

$$+ (\text{nonlinear terms})_j. \tag{B14}$$

The constant term vanishes for $j = r$ because $\phi_r(\mathbf{F}^*) = 1 - G_r(E_r^*, C_r^*) = 0$ by equation (B2), and we let $\phi_i(\mathbf{F}^*) = \mathcal{C}_i^{-i*}$, making

$$\Delta C = \mathcal{C}_i^{-i*} + [\nabla\phi_i(\mathbf{F}^*) - q_{ir}\nabla\phi_r(\mathbf{F}^*)] \cdot (\langle \mathbf{F} \rangle - \mathbf{F}^*)$$

$$+ \langle (\text{nonlinear terms})_i - q_{ir}(\text{nonlinear terms})_r \rangle. \tag{B15}$$

As is done by Chesson (2000*a*), we define $q_{ir}$ so that the linear portion in $\Delta C$ vanishes. Thus,

$$q_{ir} = \frac{\nabla\phi_i(\mathbf{F}^*) \cdot (\langle \mathbf{F} \rangle - \mathbf{F}^*)}{\nabla\phi_r(\mathbf{F}^*) \cdot (\langle \mathbf{F} \rangle - \mathbf{F}^*)} \equiv \frac{\text{linear}_i}{\text{linear}_r}. \tag{B16}$$

(See "The Effect of $\eta$ on $q_{ir}$ and $\Delta\kappa$" for a further discussion of $q_{ir}$.) Chesson (2000*a*) then defines

$$\Delta N = (\text{nonlinear terms})_i - q_{ir}(\text{nonlinear terms})_r$$

$$= \Delta C - \mathcal{C}_i^{-i*} = \langle \mathcal{C}_i \rangle - \mathcal{C}_i^{-i*} - q_{ir}\langle \mathcal{C}_r \rangle \tag{B17}$$

and

$$\tilde{\lambda}_i' - 1 = \Delta E - \mathcal{C}_i^{-i*}. \tag{B18}$$

(There, (nonlinear terms)$_j$ was approximated by the quadratic terms in the Taylor expansion of $\mathcal{C}_j$.)

An alternative definition of $\Delta I$, which shows its meaning more clearly, is

$$\Delta I = \gamma_i \operatorname{Cov}(\mathcal{E}_i, \mathcal{C}_i^{-i}) - q_{ir}\gamma_r \operatorname{Cov}(\mathcal{E}_r, \mathcal{C}_r^{-i}). \quad (B19)$$

As shown by Chesson (2000a), this definition $\Delta I$ of differs from the one above by no more than $O(\sigma^2)$.

### Calculating $\tilde{\lambda}_i'$, $\Delta N$, and $\Delta\kappa$ in the Absence of IGP

Let us now calculate the components of the invader's regional-scale growth rate when there is no IGP ($\eta = 1$). When $\eta = 1$, then resident and invader competition are the same:

$$C_{ix}(t) = C_{rx}(t) = C_x(t) = \frac{H_0\mu_{rx}}{H_x' e^{-\alpha H_x'}(1 - e^{-\mu_{rx}})}, \quad (B20)$$

and this will allow us to proceed further analytically.

For this model,

$$\mathcal{E}_{jx} = \frac{a_j H_0}{C_j^*} - 1, \quad (B21)$$

$$\mathcal{C}_{jx} = \mathcal{C}_j = 1 - \frac{a_j H_0}{C_j}. \quad (B22)$$

and $C_j^*$ should be chosen to minimize $\langle\mathcal{E}_j\rangle$. We therefore choose $C_j^* = a_j H_0$. The constant $E_j^*$ is not needed for $\mathcal{E}_{jx}$ or $\mathcal{C}_{jx}$ in this model, but it will be needed later. In order for the average of the local populations $E_{jx}\overline{P_j}$ to equal the known average $\overline{P_j}$, we must have $p_s E_{js} + p_l E_{jl} = E_j^*$. Because $p_s + p_l = 1$, we are then forced to choose $E_j^* = 1$.

The choice of $C_j^*$ causes $\langle\mathcal{E}_j\rangle$ to vanish, making $\Delta E = 0$ and leaving $\tilde{\lambda}_i' = 1 - \mathcal{C}_i^{-i*}$. In the general case with IGP, we would not be able to calculate $\mathcal{C}_i^{-i*}$ because it requires finding the equilibrium values of host and parasitoid densities when $E_r = E_r^*$, and this equilibrium cannot be found analytically. However, without IGP, $C_i(\mathbf{F}) = C_r(\mathbf{F})$,

$$\mathcal{C}_i^{-i*} = 1 - \frac{a_i H_0}{C_i(\mathbf{F}^*)} = 1 - \frac{a_i H_0}{C_r^*}, \quad (B23)$$

because by definition, $C_r(\mathbf{F}^*) = C_r^*$. We can then substitute $C_r^* = a_r H_0$ to obtain

$$\mathcal{C}_i^{-i*} = 1 - \frac{a_i}{a_r}, \quad (B24)$$

$$\tilde{\lambda}_i' = \frac{a_i}{a_r}. \quad (B25)$$

$\operatorname{Cov}(\mathcal{E}_j, \mathcal{C}_j^{-i})$ is clearly 0 because $\mathcal{E}_{jx}$ is a constant. There is, therefore, no storage effect in this model.

Equation (B16) for $q_{ir}$ relies on $\nabla\phi_i(\mathbf{F}^*)$ and $\nabla\phi_r(\mathbf{F}^*)$. We can re-express these gradients in terms of the common competition, writing

$$\nabla\phi_j(\mathbf{F}^*) = \frac{\partial\mathcal{C}j}{\partial C}\nabla C|_{\mathbf{F}=\mathbf{F}^*} = \frac{a_j H_0}{C(\mathbf{F}^*)^2}\nabla C(\mathbf{F}^*). \quad (B26)$$

Substituting into equation (B16), $H_0/C(\mathbf{F}^*)^2\nabla C(\mathbf{F}^*) \cdot (\langle\mathbf{F}\rangle - \mathbf{F}^*)$ cancels from the numerator and denominator, leaving

$$q_{ir} = \frac{a_i}{a_r}. \quad (B27)$$

Because invader competition $C_i$ and resident competition $C_r$ are the same in the absence of IGP, invader growth $\lambda_i$ and resident growth $\lambda_r$ are the same nonlinear function of the competitive factors $\mathbf{F}$. Because $\lambda_i$ and $\lambda_r$ are not nonlinear with respect to each other, relative nonlinearity $\Delta N = 0$.

Growth-density covariance is the one term that we cannot calculate analytically. We can note that relative population density $\nu_j = E_{jx}\overline{P_j}/\overline{P_j} = E_{jx}$, so using $q_{ir} = a_i/a_r$,

$$\Delta\kappa = \operatorname{Cov}(\lambda_i, E_i) - \frac{a_i}{a_r}\operatorname{Cov}(\lambda_r, E_r)$$

$$= a_i H_0\left[\operatorname{Cov}\left(\frac{1}{C}, E_i\right) - \operatorname{Cov}\left(\frac{1}{C}, E_r\right)\right]. \quad (B28)$$

This, however, is as far as we can go without resorting to numerics.

### The Effect of $\eta$ on $q_{ir}$ and $\Delta\kappa$

*Effect on $q_{ir}$.* The constant of comparison $q_{ir}$ measures the change in competition experienced by the invader relative to the change in competition experienced by the resident as their common competitive factors change. The sizes of these changes in competition are the result of both how the competitive factors change and of how sensitive competition is to these factors. Resident habitat preference determines the average resident density, which sets the values of the competitive factors, while IGP determines the values of the sensitivities.

The first competitive factor, $F_1$, is proportional to resident density and represents current competition from the resident for hosts; the second competitive factor, $F_2$, represents the effective density of hosts that can be parasitized, thus reflecting past effects of the resident. Without IGP,
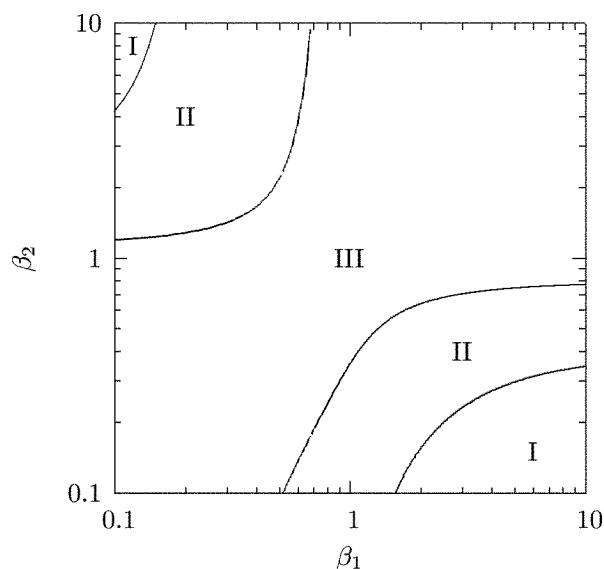
**Figure C1:** Coexistence regions with and without intraguild predation (IGP). The two species can coexist by habitat preference alone ($\eta = 1$) in the regions marked *I*. When IGP gives the inferior competitor a moderate advantage ($\eta = 0.25$), the coexistence regions expand to include the areas marked *II*. There is no coexistence in region *III*. Attack rate $a_1 = 3.5$ and $a_2 = 5.0$, host competition coefficient $\alpha = 1$, host fecundity $F = 5.0$, and the habitat is 70% leaves, 30% stems ($p_s = 0.3$, $p_l = 0.7$).

the two species depend on $F_1$ and $F_2$ in the same way, and their relative sensitivity to these common factors is determined solely by the attack rates $a_i$ and $a_r$, so $q_{ir} = a_i/a_r$. (See "Calculating $\tilde{\lambda}'_i$, $\Delta N$, and $\Delta \kappa$ in the Absence of IGP.") Adding IGP changes the invader's dependence on the competitive factors but not the resident's. Let us first consider the resident's response to the competitive factors and then the invader's.

The resident is sensitive to both $F_1$ and $F_2$, but the sensitivity to $F_1$ is overriding. This is the resident's sensitivity to its own density. An increase in the average resident density causes crowding and reduces the average resident growth rate, so the denominator of $q_{ir}$ is always negative.

As the invader becomes a stronger intraguild predator, its sensitivity to the resident density (and hence to $F_1$) decreases while its sensitivity to $F_2$ increases. Indeed, in the case where the invader is always the winner in within-host competition ($\eta = 0$ for species 1 as invader, $\eta = \infty$ for species 2 as invader), the invader is sensitive only to $F_2$. Because of the overcompensatory nature of the host competition, changes in resident density can cause post-competition host density ($F_2$) to increase or remain roughly the same. If $F_2$ changes little, then as the invader becomes a stronger intraguild predator, $q_{ir}$ declines from

a positive value to near 0 (the invader has low sensitivity to changes in competitive factors that harm the resident). If $F_2$ increases, benefiting both the invader and the resident, then a strong invader intraguild predator will experience a net benefit, not being sensitive to $F_1$, while the resident will continue to experience a net loss because its average growth is dominated by $F_1$. In this case, $q_{ir}$ becomes negative.

The opposite occurs as the invader becomes a stronger intraguild prey ($\eta = \infty$ for species 1 as invader, and $\eta = 0$ for species 2 as invader). The invader sensitivity to $F_1$ (resident density) goes up, and sensitivity to $F_2$ goes down. As a consequence, conditions that harm the resident harm the invader even more, leading to a high positive value of $q_{ir}$.

Thus, as IGP changes from favoring the resident to favoring the invader, $q_{ir}$ decreases from a positive value larger than $a_i/a_r$ toward 0 and may pass through 0 to become negative.

*Effect on $\Delta \kappa$.* Growth-density covariance $\Delta \kappa$ equals $\text{Cov}(\lambda_i, \nu_i) - q_{ir}\text{Cov}(\lambda_r, \nu_r)$. Let us consider each component in turn.

IGP has no effect on the resident's growth rate ($\lambda_r$) and thus does not affect $\text{Cov}(\lambda_r, \nu_r)$. However, as noted above, $q_{ir}$ becomes smaller when we add IGP that favors the invader. Because the resident suppresses host density in areas where it is aggregated, $\text{Cov}(\lambda_r, \nu_r)$ is negative, and thus $q_{ir}\text{Cov}(\lambda_r, \nu_r)$ increases (becomes less negative or more positive) when the invader is the intraguild predator.

Now let us turn to $\text{Cov}(\lambda_i, \nu_i)$. Adding IGP, which favors the invader, reduces the negative effects of competition with the resident, especially in the areas favored by the resident, and increases invader growth there ($\lambda_{ix}$ increases). If the resident and invader prefer different habitats ($\beta_r < 1$ in fig. 9), then $\lambda_i$ increases most in the less densely populated areas; $\text{Cov}(\lambda_i, \nu_i)$ becomes less positive and pulls $\Delta \kappa$ downward. If the resident and invader prefer the same habitat ($\beta_r > 1$ in fig. 9), then the invader's population growth ($\lambda_i$) increases most in the areas that have the greatest invader density; $\text{Cov}(\lambda_i, \nu_i)$ becomes less negative, and the invader's relative tendency to be aggregated in favorable areas is increased ($\Delta \kappa$ is pushed upward). These effects are opposite for the intraguild predator as invader, tending to increase $\Delta \kappa$ when the species have dissimilar habitat preferences.

Putting this information together, adding IGP, which favors the invader, causes $\Delta \kappa$ to decrease if the resident and invader prefer different habitats. If the two species prefer the same habitat, then the sign of $\Delta \kappa$ depends on the relative magnitude of its two constituent covariances.
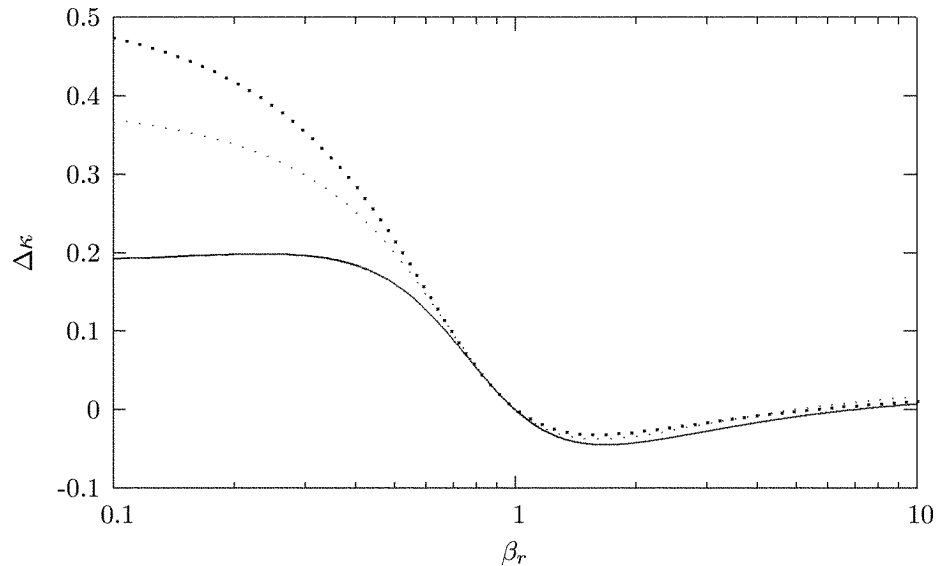
**Figure C2:** Growth-density covariance ($\Delta\kappa$) versus resident habitat preference ($\beta_r$) with and without intraguild predation (IGP). The light dotted line shows $\Delta\kappa$ in the absence of IGP (only habitat preference). The solid line shows $\Delta\kappa$ when the invader is the intraguild predator ($\eta = 0.2$), while the heavy dotted line shows $\Delta\kappa$ when the invader is the intraguild prey ($\eta = 5.0$). The invader prefers leaves ($\beta_i = \beta_1 = 5$). All other parameters are as in figure C1.

## APPENDIX C

## Varying Our Assumptions

### *Unequal Amounts of Leaf and Stem Habitat*

All of the figures in the body of the article assume that there are equal amounts of leaf and stem habitat ($p_s = p_l = 0.5$). In reality, of course, there will be more leaf habitat than stem habitat, but this does not qualitatively affect our results. The reader may compare figures C1 and C2, for which $p_s = 0.3$, $p_l = 0.7$, with figures 1 and 10, for which $p_s = p_l = 0.5$.

### *Nonconstant Attack Rates*

In this article, we contrast a nonspatial coexistence mechanism, IGP, with a spatial coexistence mechanism, the defining feature of which is that the total parasitism rate by a given species varies between habitats. We have chosen to implement this via habitat preference; species attack rates are the same in both habitats, but the amount of time they spend in each is different. This choice causes our spatial coexistence mechanism (habitat preference) to be represented primarily as a form of growth-density covariance ($\Delta\kappa$). However, we could have chosen to let the amount of time spent searching be the same across habitats but varied the attack rate between habitats, and this would have caused our spatial coexistence mechanism (spatially

varying attack rates) to be primarily a form of storage effect ($\Delta I$). The magnitude of $\Delta I$ produced by spatially varying attack rates is exactly the same as the magnitude of $\Delta\kappa$ produced by habitat preference—the coexistence mechanism is simply relabeled $\Delta I$ instead of $\Delta\kappa$—and so the coexistence region would be identical. A combination of habitat preference and spatially varying attack rates would lead to contributions to coexistence from both $\Delta\kappa$ and $\Delta I$.

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