Intraguild predation in the presence of a shared natural enemy

RICHARD J. HALL

Department of Genetics, University of Cambridge, Downing Street, Cambridge CB2 3EH United Kingdom

Abstract. Intraguild predation (IGP) is a widespread phenomenon in nature, and yet the simplest theoretical models of IGP predict that coexistence of intraguild predator and prey is only possible under restrictive assumptions. Here I examine how a specialist or generalist natural enemy of these species affects their long-term persistence and abundance, as functions of the natural enemy’s relative attack severity and fecundity on each species. Notably, I show that failure to include the effects of a higher trophic level in models of IGP can lead to incorrect predictions about the coexistence or exclusion of guild members. I then consider how an interaction between native species and a natural enemy is perturbed by the arrival of an invasive intraguild predator. I outline the conditions under which the native species and/or its natural enemy are threatened by the arrival of the intraguild predator, and also when the natural enemy is beneficial in preventing the initial invasion or eventual dominance of the invader. This work provides new insights on the influence of omnivory on food web stability, and also generates testable hypotheses for predicting the impact of a novel intraguild predator on the recipient community at multiple trophic levels.

Key words: community dynamics; competition; food webs; intraguild predation; omnivory; population dynamics; predation.

INTRODUCTION

Intraguild predation (IGP) describes an interaction in which two species that compete for shared resources also eat each other. IGP has been documented extensively in both terrestrial and aquatic communities (Polis et al. 1989), and within and between a wide variety of taxa including parasitoids and pathogens (Borer et al. 2007). In cases where IGP is predominantly unidirectional, the consumer and victim are referred to as the IG predator and IG prey, respectively. In an analysis conducted across 113 food webs, the observed frequency of IGP among all potential IG predator and prey combinations was found to lie between 58.4% and 86.7%, suggesting that IGP is both widespread and common (Arim and Marquet 2004). Holt and Polis (1997) outlined a theoretical framework for IGP, and paradoxically, showed that stable coexistence of IG predator and prey occurs only under restrictive conditions: specifically, coexistence is possible only when the IG prey is a superior competitor of the shared basal resource, and at intermediate resource productivity. Resolving the mismatch between theory and empirical evidence has stimulated the development of new models aiming to explain coexistence by including more details of the life histories of the IG predator and prey (van de Wolfshaar et al. 2006, Yamaguchi et al. 2007) or their shared resources (Daugherty et al. 2007, Holt and Huxel 2007, Kimbrell et al. 2007), and by explicitly considering spatiotemporal processes such as dispersal (Amarasekare 2007, Bampfyldle and Lewis 2007) or temporal niche overlap (Amarasekare 2008).

Holt and Polis (1997) noted that “most IGP systems are embedded in speciose food webs.” In particular, IGP is frequently documented as occurring within invertebrate guilds or between invertebrates and their vertebrate predators (Vance-Chalcraft et al. 2007, Mooney et al. 2010). Given that these species typically occur at intermediate trophic levels, it is perhaps surprising that relatively few studies have explicitly investigated how a shared predator or parasite of species engaged in IGP can affect their dynamics (but see Hatcher et al. 2008). As a motivating example, the recent arrival of the Asian ladybird beetle Harmania axyridis in the United Kingdom has sparked concerns for native entomophagous ladybirds, with which it has complete dietary overlap and engages in unidirectional larval IGP (Ware and Majerus 2008). Following the introduction of Harmonia axyridis in the USA, native ladybird abundance and local species richness decreased (Snyder et al. 2004), both of which have been shown to reduce the overall efficacy of biocontrol of aphid crop pests (Rosenheim et al. 1995). However, successful field parasitism of H. axyridis by a parasitoid of native British ladybirds (Dinocampus coccinellae) has recently been recorded (Hall et al. 2009). In the best-case scenario, the natural enemy may regulate the population of the novel IG predator and increase the density of the native IG prey through apparent competition; less desirable outcomes include an increase in the enemy...
population leading to higher attack rates on the IG prey, or the enemy itself may be threatened if it has low fecundity on the novel host. Thus, developing a theoretical framework for the dynamics of IGP with a shared natural enemy not only enhances our mechanistic understanding of food web complexity and stability, but is also of applied importance for predicting whether native communities are resilient to the effects of invasive IG predators.

Here I develop models for the interaction of IG predator and prey subject to attacks by a generalist or specialist natural enemy, where “specialist” is defined such that the IG predator and IG prey are the only two resources available to the natural enemy. I identify the model equilibria and their stability as functions of the relative severity of enemy attack on the IG predator and prey, and the enemy’s relative fecundity on each species under a variety of scenarios for the interaction between the IG prey and predator. For the case of a novel IG predator invading a host-enemy interaction, I relate these parameters to the equilibrium population sizes before and after invasion, and the time until the IG prey is reduced to a small fraction of its preinvasion density. The results are interpreted in the context of previous studies on three-species interactions, food web omnivory and stability, and the likely impacts of an invasive IG predator on native community structure.

**Model and Methods**

**Model assumptions and derivation**

A schematic of the IG predator–IG prey–natural enemy interaction is given in Fig. 1a. I use a system of ordinary differential equations to describe the population dynamics of the IG prey (with population density \( N_1 \)), IG predator (density \( N_2 \)), and natural enemy (density \( P \)). The natural enemy may be a predator or a parasitoid, but for the latter case the time between parasitoid attack and host death is assumed to be short relative to the life spans of the host species. Following Hatcher et al. (2008), competition for shared resources between the IG predator and prey is modeled as Lotka–Volterra competition. As well as reducing model complexity to focus on the dynamical effects of a higher trophic level, this is a more realistic assumption when resource overlap is not complete. IGP and natural enemy attack rates are modeled as Lotka–Volterra competition. As well as reducing model complexity, this is a more realistic assumption when resource overlap is not complete. IGP and natural enemy attack rates are modeled as Lotka–Volterra competition.

Under these assumptions the equations for the dynamics of the IG prey and predator are given by, respectively,

\[
\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 - \alpha_{12} N_2) - \lambda N_1 N_2 - \beta_1 N_1 P
\]

\[
\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{21} N_1 - \alpha_{22} N_2) + \varepsilon \lambda N_1 N_2 - \beta_2 N_2 P
\]

where the \( r_i \) are the intrinsic growth rates of species \( i \), \( \alpha_{ij} \) measures the competitive effect on species \( i \) of species \( j \), \( \lambda \), is the IG predation rate, and IG prey is converted into new IG predators with efficiency \( \varepsilon \). The attack rate on species \( i \) by the natural enemy is \( \beta_i \). If the natural enemy attacks a wide range of species, its population size is unlikely to be greatly affected by changes in the populations of the IG predator and prey, and so we can assume that \( P \) is approximately constant. In the case of a specialist enemy of the IG prey and/or IG predator, the prey dynamics are described by

\[
\frac{dP}{dt} = c_1 \beta_1 N_1 P + c_2 \beta_2 N_2 P - \mu P
\]
where $e_i$ is the conversion efficiency of species $i$ into the natural enemy and $\mu$ is the enemy mortality rate.

**Model rescaling and key parameters**

Despite the relative simplicity of the two models described above, they are nonetheless parameter rich (10 parameters for the generalist enemy model, 13 for the specialist). Non-dimensionalization is a powerful technique for rescaling the model variables to reduce the number of parameters to a set of key agglomerate parameters that drive the model dynamics, while maintaining biological relevance (Murray 1989). Denoting the scaled model variables with italics, I rescale the densities of the IG predator and prey by their respective carrying capacities ($N_i = [1/\alpha_i]N_i$), time relative to the growth rate of the IG prey ($t = [1/r_1]t$) and the natural enemy density by the ratio of the IG prey growth rate to the enemy attack rate on the IG prey ($P = [r_1/\beta_1]P$). The rescaled dynamics of IG prey and predator are given by

$$\frac{dN_1}{dt} = N_1(1 - N_1 - c_1N_2 - P)$$

$$\frac{dN_2}{dt} = \rho N_1(1 - c_2N_1 - N_2 - \phi P)$$

and for a specialist natural enemy

$$\frac{dP}{dt} = \nu P[R(N_1 + \theta N_2) - 1].$$

The number of model parameters to consider has been greatly reduced (four for the generalist model, seven for the specialist model; see Table 1). I outline the biological meaning of these parameters below; a more detailed explanation of the rescaling and how the agglomerate parameters relate to the original model parameters is given in Appendix: Model rescaling and Parameter definitions and interpretation.

The parameter $c_i (i = 1, 2)$ measures the net effect of IGP on species $i$ of its interaction with the other guild member through competition and predation. It is scaled so that $0 < c_i < 1$ represents a relatively weak interspecific interaction, while $c_i > 1$ means that the other guild member exerts a larger per capita effect on species $i$'s growth rate than it does on its own growth rate. For the IG predator, $c_2 < 0$ indicates that the benefits of consuming the IG prey outweigh the costs of interspecific competition for shared resources; increasing the IG predation rate simultaneously increases $c_1$ and reduces $c_2$. The parameter $\rho$ is the intrinsic growth rate of the IG predator relative to that of the IG prey; it takes values close to one if the two species have similar life histories, while very large or very small values may reflect that they differ strongly in life history and/or acquisition rates of basal resources. The parameter $\phi$ measures the relative attack severity of the natural enemy on the IG predator; $\phi > 1$ indicates that the IG predator suffers a larger per capita reduction in its growth rate through enemy attack than the IG prey. This may reflect that the IG predator is preferentially attacked by the enemy, or that it has a lower intrinsic growth rate than the IG prey (and therefore its population takes longer to recover in response to changes in the enemy density). The lifetime reproductive success of the enemy when introduced to the IG prey population at its carrying capacity is given by $R$, and must be greater than one for the enemy to persist on the IG prey alone; $\theta$ measures the enemy’s relative fecundity on the IG predator, with $\theta > 1$ indicating that the IG predator is a higher quality resource for the enemy. An enemy attack preference for the IG predator, higher conversion efficiency of the IG predator, or a larger carrying capacity of the IG predator compared with the IG prey all result in larger values of relative fecundity. Finally $\nu$ is the ratio of the per capita enemy mortality rate to the IG prey’s intrinsic growth rate; values differing substantially from one reflect differences in the timescales over which the IG prey and natural enemy respond to changes in the densities of interacting species.

**Methods**

I explore the effects of a shared natural enemy on the IG predator and prey by considering three qualitatively different scenarios for the IGP interaction: (1) weak...
interspecific interactions \((0 < c_1, c_2 < 1)\), where IG predator and prey are expected to coexist in the absence of the enemy; (2) the IG predator experiences a net benefit from its interaction with the IG prey \((c_2 < 0)\), i.e., the interaction is more predation-like than competition-like; and (3) the IG predator has a strong negative effect on the IG prey density \((c_1 > 1)\), so that the IG predator excludes the IG prey in the absence of the enemy. The effects of a generalist natural enemy are modeled by varying the predator density \((P)\) and the relative attack severity on the IG predator \((\phi)\). For the specialist natural enemy I consider three scenarios for the natural enemy fitness on the IG predator and prey: the natural enemy can persist on either species \((R, R > 1)\) but has higher fecundity on (1) the IG predator \((\theta > 1)\), (2) the IG prey \((\theta < 1)\), or most pertinent to an IG predator invading a native IG prey–enemy interaction, (3) the enemy is unable to persist on IG predator alone \((R > 1\ \theta R)\). How each of these scenarios relates to interaction strengths between species is summarized in Fig. 1b.

The model equilibria are calculated exactly as functions of the agglomerate parameters, and conditions for their stability outlined in section iii of the Appendix. It is instructive to calculate these equilibrium abundances even when the dynamics do not converge to an equilibrium point (e.g., limit cycles), since they also describe the average population sizes along such trajectories (Hofbauer and Sigmund 1998). In order to understand the effects of an introduced IG predator invading a prey–enemy interaction, I compare the equilibrium population sizes before and after the invasion. I solve the differential equations numerically to calculate the time until the IG prey declines to 5% of its preinvasion density using the ode45 differential equation solver in MATLAB (release 2009a; The MathWorks, Natick, Massachusetts, USA). In numerical solutions, I have assumed that the dynamics of the IG predator, IG prey, and natural enemy occur over comparable timescales (i.e., \(p, v \approx 1\)). This assumption has little effect on the equilibrium population sizes and their stability, but will impact the speed at which equilibria are approached.

RESULTS

Generalist natural enemy

When the IG predator and prey are attacked by a generalist natural enemy, there are four possible stable equilibrium states: stable coexistence of IG predator and prey, exclusion of the IG prey or IG predator, or exclusion of both species. Exact expressions for these equilibrium densities in terms of the model parameters are outlined in the Appendix (Table A1). Persistence of the IG predator, prey or both species is dependent on their ability to increase in number when introduced to the other species at its equilibrium density; in other words, the combined effects of IGP \((c_1, c_2)\) and enemy attack \((P, \phi)\) on its per capita growth rate must be relatively small.

![Fig. 2. Effect of a generalist natural enemy on the long-term persistence of the IG predator and prey, in terms of the enemy’s attack rates on each. The diagonal line separates the regions in which the natural enemy has a larger negative effect on the IG predator (\(\phi > 1\), top left) or IG prey (\(\phi < 1\), bottom right). Long-term coexistence of the IG predator and prey is possible in the white region, one species persists in the light gray regions, and both species perish in the dark gray region. Moderate levels of IGP and interspecific competition are assumed \((0 < c_1, c_2 < 1\) such that the IG predator and prey coexist in the absence of the natural enemy. When the IG predator gains a net benefit from consuming the IG prey \((c_2 < 0\), the upper bound of the coexistence region extends to the dashed line. When IGP excludes the IG prey in the absence of the natural enemy \((c_1 > 1\), coexistence is restricted to the white region above the dotted-and-dashed line.

1. Weak IGP \((0 < c_1, c_2 < 1)\).—When the effects of the IGP interaction on the IG predator and prey growth rates are weak relative to the effects of intraspecific density dependence, the IG predator and prey are expected to coexist in the absence of the natural enemy. Increasing the natural enemy attack rates on one or both species decreases the possibility of coexistence of IG predator and prey (Fig. 2). The equilibrium density of the IG prey is an increasing function of the enemy’s relative attack severity on the IG predator \((\phi)\), while the equilibrium IG predator density is a decreasing function (Fig. 3a). There are threshold values of the relative attack severity below which the IG prey is excluded and above which the IG predator is excluded; the two species coexist when \(\phi\) lies between these values. For the case of an introduced IG predator invading a native enemy–IG prey interaction, the post-invasion equilibrium density of the IG prey is lower than its preinvasion density whenever the IG predator is able to invade (i.e., below the threshold value of relative attack preference at which the IG predator is excluded). The time taken until the IG prey has declined to 5% of its preinvasion density is a faster than linearly increasing function of the relative
attack severity, with an asymptote when the attack severity is large enough for the IG predator and prey to coexist (Fig. 3d). However, rapid decline of the native IG prey can occur when enemy attack rates on the introduced IG predator are low.

2. **IG predator receives a net benefit from the IGP interaction** \((c_2 < 0)\).—When the benefit to the IG predator from consuming the IG prey outweighs the cost of interspecific competition for basal resources, it is possible for the IG predator to persist under higher levels of natural enemy attack than it could survive in the absence of the IG prey \((\phi P > 1)\). When compared with the weak IGP interaction above, coexistence of the IG predator and prey occurs over a larger range of the relative attack severity on the IG predator (Fig. 3b). However, the post-invasion density of the IG prey remains lower than its preinvasion density over this range, and the time until it declines to 5% if its preinvasion density is shorter (Fig. 3d).

3. **Strong effect of IG predator on IG prey** \((c_1 > 1)\).—In the absence of the natural enemy, the effect of IGP is sufficiently strong that IG prey is always excluded. The natural enemy may permit coexistence of the IG predator and prey over a limited range of the relative attack severity on the IG predator, provided that the enemy has a stronger effect on the IG predator’s growth than on the IG prey’s growth \((\phi > 1\), Fig. 2). Exclusion of the IG prey post-invasion occurs at larger values of

Fig. 3. Effect of the relative attack severity \((\phi)\) on the equilibrium densities of IG predator (thick lines) and prey (thin lines) as a fraction of their respective carrying capacities under the following conditions: (a) a weak IGP interaction \((c_1 = 0.8, c_2 = 0.6)\); (b) the IG predator receives a net benefit from IGP \((c_1 = 0.8, c_2 = -0.2)\); and (c) IGP has a strong negative effect on the IG prey \((c_1 = 1.2, c_2 = 0.6)\). The natural enemy attack rate on the IG prey, \(P = 0.5\). (d) Effect of enemy attack preference on the time until the IG prey has declined to 95% of its initial density when IGP is weak (bold line), the IG predator receives a net benefit from IGP (dashed line), and IGP has a strong negative effect on the IG prey (dots and dashes). One unit of time is equal to the inverse of the IG prey growth rate. Parameter values are as above; additionally the intrinsic growth rates of the IG predator and prey are equal \((\rho = 1)\). Initially the IG prey is at its equilibrium with the generalist natural enemy, and the IG predator is introduced at 1% of its carrying capacity \([N_1(0) = 0.5, N_2(0) = 0.01]\).
the relative attack severity than the previous two examples, and the transition between native extirpation and invasion resistance as a function of relative attack severity is sharper (Fig. 3c). The time until 95% decline of the IG prey is always shorter than under weak IGP, and the range of relative attack severity over which this decline occurs is greater (Fig. 3d).

**Specialist natural enemy**

1. **Species persistence.**—There are six possible equilibria corresponding to the persistence of one, two, or three species. The analytical conditions for their local stability in terms of the model parameters are outlined in the Appendix (Table A2). Depending on the model parameters, the system may have a single globally stable equilibrium, two locally stable equilibria with the eventual outcome determined by the initial conditions, or persistence of the three species via sustained cycles (Fig. 4).

If the enemy has higher fecundity on the IG predator than on the IG prey \((h > 1)\), the species persisting at equilibrium switch from IG predator–enemy, through three-species coexistence, to IG prey–enemy as the relative severity of enemy attack on the IG predator \((\varphi)\) increases. Consistent with the results for the generalist natural enemy, I found that three-species...
coexistence was likely over a larger region of parameter space if the IG predator gains a net benefit from IGP (Fig. 4b), and that enemy-mediated coexistence of IG predator and prey was still possible over a small range of the relative attack severity when IGP has a strong negative effect on the IG prey (Fig. 4c).

If the natural enemy has low fecundity on the IG predator \((0R < 1)\), the arrival of an invasive IG predator may result in the enemy’s extinction if the IG predator severely reduces the abundance of its native prey. Further, if the effects of IGP on the IG prey are strong, only the IG predator persists; this demonstrates how an invasive IG predator can cause extinctions at multiple trophic levels (Fig. 4c). In the case where the natural enemy attacks the introduced IG predator at a high rate (i.e., \(\phi \) is large), but has low fecundity on it, the native prey-enemy equilibrium may be able to resist invasion provided the initial density of the IG predator is low.

The model permits cyclic persistence of all three species; however I found the regions of parameter space in which cycles occurred to be small (Fig. 4d), and therefore unlikely to be observed in natural systems that are adequately described by this model. While the exact conditions for cycles to occur are not readily open to biological interpretation (see Appendix: Model equilibria and stability), numerical solutions of the model over parameter combinations for which the three-species equilibrium exists but is unstable revealed that the following conditions are conducive to limit cycles: (1) the IG predator and prey cannot coexist in the absence of the natural enemy; (2) the enemy can persist on the winner of the IG predator interaction alone, and not on the loser alone; and (3) attack severity is stronger on the winner than on the loser.

2. Effect of invasive IG predator on population sizes.— If the IG predator is able to invade (i.e., the relative attack severity is sufficiently low), the post-invasion density of the IG prey is lower than its preinvasion density (Fig. 5). When the enemy has higher fecundity on the introduced IG predator than its native prey \((0R > R > 1)\), the enemy density is a decreasing function of its relative attack severity on the IG predator (Fig. 5a–c). The enemy density remains higher than its preinvasion density over the largest range of attack severity when the IG predator gains a net benefit from its interaction with the IG prey, and declines fastest to its preinvasion density when the IG predator has a strong negative effect on the IG prey.

When the enemy has higher relative fecundity on the IG prey \((R > 0R > 1)\), its post-invasion density is lower than its preinvasion density whenever the three species coexist (Fig. 5d–e). When the effect of IGP on the IG prey is strong, the IG prey and enemy either resist the invasion with their densities remaining at the preinvasion level, or the IG prey is extirpated and the enemy persists at a much lower density (Fig. 5f).

When the enemy is unable to persist on the IG predator alone \((0R < 1)\) and the IGP interaction is weak, the IG prey and enemy coexist with the IG predator at densities lower than their preinvasion level when the relative attack severity is low, or resist invasion when the attack severity is high (Fig. 5g). If the IG predator gains a net benefit from IGP, the enemy is extirpated and the equilibrium IG prey density is lower than its preinvasion density (Fig. 5h). When IGP has a strong negative effect on the prey, both the enemy and IG prey are excluded at low values of the enemy attack severity, and the IG predator attains its carrying capacity (Fig. 5i).

3. Effect of invasive IG predator on time to 95% decline of IG prey.—As seen for the generalist natural enemy, the IG prey persisted at high density for longer, and over the largest range of relative attack severity on the IG predator, when IGP was relatively weak (Fig. 6). Severe declines in the IG prey were noted over the largest range of \(\phi \) when the effects of IGP on the IG prey were strong. Unlike the generalist case, declines in the IG prey occurred most rapidly when both the relative attack severity is low, and the IG predator derives a net benefit from IGP. Decreasing the enemy’s relative fecundity on the IG predator in general decreased the rate of decline of the IG prey, and increased the range of values of the relative attack severity over which this decline was prevented.

**DISCUSSION**

**Effects of a natural enemy on the IGP interaction**

In this article, I have investigated how a species at a higher trophic level affects the interaction between IG predator and prey. I found that failing to include the effects of a natural enemy results in incorrect predictions about which species persist, and their relative abundance. Holt and Polis (1997) developed models of IGP showing that coexistence of IG predator and prey can only occur if the IG prey is a superior competitor of the basal resource it shares with the IG predator. My primary finding is that a specialist or generalist natural enemy that has a larger effect on the dynamics of the IG predator than the IG prey (e.g., through preferentially attacking it) can mediate coexistence when the IG predator is predicted to exclude the prey in the absence of the enemy. This conclusion is supported by a previous study on an IGP system with a shared microparasite (Hatcher et al. 2008).

**Relation to other three-species interactions**

The IGP module with a specialist natural enemy investigated in this article bears similarities to other, well-studied systems of three-species interactions. If the effect of IGP on the densities of IG predator and prey is weak, the behavior of system is identical to a two-competitor one-predator model. Consistent with theory (Holt 1977) and empirical observations (Vance 1978) of apparent competition, the enemy density increases if it has higher relative fecundity on one species, which in turn lowers the density of the inferior resource.
Increasing the level of IGP simultaneously increases the IG predator’s negative impact on the prey ($c_1$), and decreases the impact of the IG prey on the predator ($c_2$). The net result is an increase in the threshold values of the relative attack severity below which only the IG predator persists, and above which the IG prey persists; in other words, three-species coexistence is only likely when the effect of enemy attack was more severe on the IG predator than the IG prey.

When the enemy exhibits a strong preference for attacking the IG predator, the IGP module resembles a three-species food chain. Consistent with the concept of a trophic cascade (Hairston et al. 1960), increasing the enemy’s attack severity on the IG predator reduces the equilibrium IG predator density, resulting in an increase in the IG prey density. Conversely, when the enemy preferentially attacks the IG prey, the interaction more closely resembles a two-predator–one-prey system, in which only one of the predators is expected to persist under the competitive exclusion principle (Hardin 1960). Indeed, when the enemy’s relative attack preference and fecundity on the IG predator are low, the natural enemy is always excluded. The natural enemy always loses out since the IG prey is its only viable resource, while the IG predator is able to survive on basal resources when the IG prey density is very low. The ability of the IG predator to maintain a high density on the basal resources mean that high levels of IGP and/or competition can also lead to the exclusion of the IG prey.

**IGP and food web stability**

In a model of IGP with a single basal resource growing logistically, and non-saturating predation functional responses, Tanabe and Namba (2005) showed that IGP could destabilize the coexistence equilibrium resulting in limit cycles or chaotic dynamics.
Conversely, the addition of omnivory has been shown to have a stabilizing effect on unstable three-species food chains with saturating functional responses (McCann and Hastings 1997). I found no evidence of cyclic behavior under a generalist natural enemy, while cycles were only possible over a small range of parameter combinations for a specialist natural enemy. The scarcity of cyclic dynamics in this study may be a consequence of the “mass-action” assumption for how competition for basal resources was modeled (Ruggieri and Schreiber 2005). In agreement with McCann and Hastings (1997), and with recent network theory in larger scale food webs (e.g., Dunne et al. 2002), the addition of trophic links in this model (i.e., increasing connectance) enabled three-species coexistence where it would not otherwise be possible: natural enemy attack on the IG predator prevented it from excluding the IG prey, while supplementary feeding on the IG prey allowed the IG predator to persist at levels of enemy attack at which it would otherwise be excluded.

**IGP and biological invasions**

The results presented here generate the following hypotheses relating to the community response to the introduction of a novel intraguild predator. These hypotheses should be testable in empirical systems provided crude estimates of the native and invader's relative competitive ability, IGP rate, and the natural enemy's attack rates and fecundity on each species are amenable to measurement.

1) The native community is likely to resist invasion by an introduced IG predator if a native enemy of the IG prey preferentially attacks the IG predator.

2) If an IG predator is able to invade, the post-invasion equilibrium density of the IG prey is always lower than its preinvasion density. The enemy density will be higher (lower) than its preinvasion density if its fecundity on the IG predator is higher (lower) than on the native IG prey.

3) Low enemy attack rates and relative fecundity on an introduced IG predator can result in the exclusion of the enemy, and if the IGP interaction is strong, the IG prey will also be excluded.

While in systems where the IG predator, prey, and natural enemy have coevolved, one would expect the enemy's relative attack severity and relative fecundity to be positively correlated, this is not necessarily the case for a natural enemy exploiting a novel prey item. In particular, false cues of prey quality or a lack of enemy-evasion strategies in the introduced species may initially result in high relative attack rates but low enemy fecundity, in which case the ultimate outcome of the invasion (invasion resistance or native enemy extinction) depends on the invader density. While invader eradication is often technically difficult and costly, such a situation may be more amenable to successful management, since a sufficient reduction in the invader density...
allows the native community to recover and resist future invasion (Bampfylde and Lewis 2007).

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**Literature Cited**


