A THEORETICAL FRAMEWORK FOR INTRAGUILD PREDATION

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Abstract.—Many important issues in community ecology revolve around the interplay of competition and predation. Species that compete may also be locked in predator-prey interactions, a mixture of competition and predation known as "intraguild predation" (IGP). There is growing evidence for the importance of IGP in many natural communities, yet little formal ecological theory addresses this particular blend of interactions. In this article, we explore the consequences of incorporating IGP into standard models of exploitative competition and food chains (a general resource-consumer model, a Lotka-Volterra food chain model, and Schoener's exploitative competition model). Our theoretical analyses suggest a general criterion for coexistence in IGP systems: the intermediate species (the prey in intraguild predation) should be superior at exploitative competition for the shared resource, whereas the top species (the predator) should gain significantly from its consumption of the intermediate species. Along gradients in environmental productivity, coexistence is most likely at intermediate levels of productivity. Analyses of the models reveal the potential for alternative stable states in systems with IGP; these are particularly likely if the top predator gains little benefit from consuming the intermediate predator. We further show that IGP can lead to unstable population dynamics, even when all pairwise interactions are inherently stable and each species can increase when rare. Persistent, strong IGP raises a puzzle of species coexistence, particularly in productive environments. We conclude by comparing IGP with related community modules (i.e., food chains, exploitative competition, apparent competition) and discussing mechanisms that should foster coexistence in systems with strong IGP.

Predation and competition have long been mainstays of ecological research, in part because they constitute the building blocks for complex, multispecies food webs (e.g., DeAngelis 1992; Polis and Winemiller 1995). Yet entire food webs, taken as a whole, are rather unwieldy units for detailed analyses (Polis 1994). At an intermediate level of complexity—between the simplicity of pairwise interactions and the baroque complexity of fully specified food webs (e.g., Polis 1991)— are "community modules" (see, e.g., Holt et al. 1994), defined by strong interactions among a small number of species (Holt 1996). Analyses of modules are interesting in their own right, for they often describe interaction patterns in sub-webs of natural communities (Menge 1995). Moreover, analyses of modules shed light on processes operating in more complex assemblages.

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One important community module that has received considerable attention from theoretical and empirical ecologists is competition among species in one trophic level, modulated by predation from species at a higher trophic level (see, e.g., Armstrong 1979; Holt 1985; Yodzis 1986; Holt et al. 1994; Leibold 1996). The interplay of competition and predation can greatly influence species coexistence or exclusion, and thus community composition (e.g., via the keystone predator effect [Leibold 1996] or apparent competition [Holt 1984; Holt and Lawton 1994]). Theoretical studies have also highlighted the potential importance of combined predation and competition for population dynamics. For instance, even a simple Lotka-Volterra model of a predator consuming two competing prey—in which all pairwise interactions are well behaved (settling into stable equilibria)—can exhibit limit cycles or chaotic dynamics (Gilpin 1979).

There is another, quite distinct way to mix up predation and competition: species that compete for resources may also engage in direct predator-prey interactions. This leads to the community module we have christened intraguild predation (IGP; Polis et al. 1989; Polis and Holt 1992). We define IGP as the killing and eating of prey species by a predator that also can utilize the resources of those prey (Polis et al. 1989); hence, the predator and prey species are also potentially exploitative competitors. Intraguild predation is a subset of omnivory, which is defined as feeding on resources at different trophic levels.

There are numerous examples of strong IGP from natural communities (Polis et al. 1989). Indeed, in some systems this module is a dominant theme in community organization (e.g., Polis and McCormick 1986, 1987; Schoener and Spiller 1987; Barkai and McQuaid 1989; Johnson 1991; Posey and Hines 1991; Purcell 1991; Wissinger 1992). Many important problems in applied ecology involve a significant component of IGP (for examples, see Barkai and McQuaid 1989; Valdes Szeinfeld 1991; Ehler 1992, 1995; Polis and Holt 1992; Rosenheim et al. 1993; Laurenson 1995). Yet little explicit theory has focused on IGP (see, however, Pimm and Lawton 1977; Rosenzweig 1977; May and Hassell 1981; Pimm 1991). Diehl (1995) recently remarked that mathematical models have barely been formulated for IGP, despite its commonness in natural communities. This is a striking lacunae in theoretical ecology, particularly given the large corpus of work examining effects of predation on competing prey (e.g., Yodzis 1986; Holt et al. 1994).

Our purpose here is to explore systematically the consequences of incorporating IGP into familiar models of competition and predation, so as to begin to develop a conceptual framework to analyze the population- and community-level implications of IGP. The theoretical analyses that we present help clarify the conditions for coexistence in systems with IGP and highlight the rich potential for alternative stable states. We show that IGP can generate unstable dynamics, which can lead to transient phases of low population densities and a heightened risk of extinction. A problem of species coexistence thus arises whenever one observes a system with strong, persistent IGP. In the Discussion, we compare our IGP models with models of other, related community modules (in particular, food chains, exploitative competition, and apparent competition) and sketch directions for future theoretical investigations.

IGP IN MECHANISTIC MODELS OF RESOURCE COMPETITION

In models of IGP, it is important that the formalism chosen does not confuse the direct effects of the predator-prey interaction with the indirect effects of exploitative competition. The approach we take is to introduce terms representing IGP into well-known mechanistic models for resource competition and food chain dynamics (Schoener 1986; Tilman 1987). For convenience, henceforth the top predator will be called the IGpredator and the intermediate predator, the IGprey. The IGpredator is an oligophage completely dependent on the IGprey and the basal resource for its sustenance; the IGprey is a specialist on the basal resource. Consider the following model:

$$\frac{dP}{dt} = P[b'a'(R, N, P)R + \beta\alpha(R, N, P)N - m'],$$

$$\frac{dN}{dt} = N[ba(R, N, P)R - \alpha(R, N, P)P - m], \tag{1}$$

and

$$\frac{dR}{dt} = R[\phi(R) - a(R, N, P)N - a'(R, N, P)P].$$

The densities of the IGpredator, IGprey, and basal resource are, respectively, P, N, and R. The quantities $a'(R, N, P)R$ and $\alpha(R, N, P)N$ are functional responses of the IGpredator to the resource and IGprey, respectively; $a(R, N, P)R$ is the functional response of the IGprey to the basal resource; and m and m' are density-independent mortality rates. The parameters b and b' convert resource consumption into reproduction for the IGprey and IGpredator, respectively; the parameter β scales the benefit enjoyed by the IGpredator from its consumption of IGprey. We deliberately use the symbol α to denote mortality inflicted on the IGprey by the IGpredator, because in some circumstances such mortality could be viewed as interspecific interference competition (Gill 1974; Polis 1988) and might be measured by a competition coefficient (even though the actual mechanism is mortality from predation). Finally, $R\phi(R)$ is recruitment of the basal resource.

Model (1) can encompass many scenarios: for instance, an optimally foraging IGpredator might drop the IGprey from its diet, given an abundant basal resource. Rather than deal with the model in its full generality, we examine three illustrative cases that capture important qualitative aspects of IGP. The first model, a re-source-consumer model including IGP, leads to a general coexistence criterion. The second model adds IGP to a standard Lotka-Volterra model for a food chain; this model can display complex dynamic behaviors and highlights the possibility of alternative stable states (with or without the IGprey). The third model adds IGP to Schoener's (1974, 1976) model for exploitative competition. In this model, alternative stable states arise, such that qualitatively distinct kinds of net interspecific interactions can occur in a single system.

General Additive Model

Mechanistic models of purely exploitative competition (Tilman 1982; DeAngelis 1992) include an expression for the per capita growth rate of each competing consumer (at density N_i) as a function of resource availability, R, and an equation for resource dynamics:

$$\frac{dN_i}{dt} = N_i f_i(R), \quad \frac{dR}{dt} = R\phi(R) - \sum_i c_i R, \quad i = P, N,$$

where c_i is the per-unit resource rate of consumption by consumer i.

Assume that f_i increases with R and that some value R_i^* exists such that consumer i is in equilibrium; that is,

$$\frac{dN_i}{dt} = N_i f_i(R_i^*) = 0.$$

A general rule of thumb for dominance in exploitative competition is that the consumer species persisting at the lowest resource level wins (the R^* rule; Tilman 1990).

The simplest way to incorporate IGP into exploitative competition models is to splice predator-prey terms into the growth equations for each competitor, as follows (where P and N denote the IGpredator and IGprey, respectively):

IGpredator: $dP/dt = P\{f_P(R) + g_P[\alpha(P, N, R)N]\}$;

IGprey: $dN/dt = N[f_N(R) - \alpha(P, N, R)P]$. $\qquad$ (2)

The function g_P describes how the per capita growth rate of the IGpredator is enhanced by consuming the IGprey. We assume that $g_P > 0$ and that this component of growth increases with the per capita rate of consumption of the IGprey by the IGpredator, $\alpha(R, N, P)N$. The per-prey mortality imposed on the IGprey by the IGpredator is $\alpha(R, N, P)P$.

An important subtlety in the interpretation of g_P should be stressed to forestall possible misunderstanding (e.g., Diehl 1993). Model (2) expresses the demographic effect of IGP for the IGpredator as a positive term, measured against a basal growth rate on the resource (at level R). This net demographic effect encompasses both direct caloric benefits provided by the consumption of the IGprey and any costs due to reduced intake of the basal resource (e.g., because of time spent handling the IGprey, reducing the time available to search for the basal resource). This model thus assumes the IGpredator enjoys an overall, instantaneous positive benefit from its consumption of the IGprey; otherwise, such consumption would be maladaptive for the IGpredator, and the IGprey should be dropped from its diet. Predators may for various reasons have suboptimal diets (see Holt 1983); the following conclusions need not apply to IGP systems with such predators.

This model illustrates the simple, intuitive, but nonetheless fundamental point that for an IGP system to persist with all species, the IGpredator must be inferior

at exploiting the shared resource (Polis and Holt 1992). At an equilibrium, assuming one exists, it is necessary that

$$f_P(R^*) = -g_P[\alpha(P^*, N^*, R^*)N^*] < 0$$

and (3)

$$f_N(R^*) = \alpha(P^*, N^*, R^*)P^* > 0 .$$

Hence, $f_N(R^*) > 0 > f_p(R^*)$. This states that, given the ambient level of resources at equilibrium with all species present, the IGpredator would decline, were it supported by just the basal resource. Moreover, the IGprey could increase, were it not for predation from the IGpredator. This inequality operationally defines superiority in resource exploitation by IGprey at the joint equilibrium.

This does *not* necessarily imply that the IGprey more rapidly depletes the resource. Rather, the inequality (3) reflects how each exploiter tolerates resource limitation. Such tolerance involves both resource uptake and resistance to factors of density-independent mortality. If $f_N(R) < f_P(R)$ for all R, the IGpredator is superior in resource competition; in this case, the IGprey tends to be excluded by the IGpredator even in the absence of direct predation, and IGP only hastens exclusion.

Without the IGpredator, the IGprey grows at the resource level of R^*, ultimately depressing resources to a lower level, say, $R_N^* < R^*$ (more precisely, R_N^* is the solution of $f_N(R) = 0$ and indicates the level of resources needed to sustain the IGprey, when the IGpredator is absent). Without the IGprey, the IGpredator cannot persist at resource level R^* and declines until the basal resources increase to $R_P^* > R^*$ (R_P^*, the solution of $f_P(R) = 0$, defines the resource availability required to support the IGpredator without IGprey). Putting these facts together leads to

$$R_N^* < R^* < R_P^* . \tag{4}$$

This states that the IGprey is superior at exploitative competition (using the R^* rule; Tilman 1990; Holt et al. 1994; Grover 1995). Inequality (4) provides a general, necessary criterion for coexistence of a resource-limited IGpredator and IGprey both solely dependent (directly or indirectly) on the same basal resource. Deriving sufficient conditions for coexistence in IGP systems requires more specific models. We now consider two examples.

A Lotka-Volterra IGP Model

For simplicity, assume interactions are linear (on a per capita basis). In particular, let $\phi(R) = r(1 - R/K)$, $a(P, N, R) \equiv a$, $a'(P, N, R) \equiv a'$, and $\alpha(P, N, R) \equiv \alpha$; the basal resource when alone grows according to a logistic model, each consumer has linear functional responses, and consumer growth is proportional to the rate of consumption. In effect, we add IGP to a standard Lotka-Volterra

model for a food chain (e.g., Hallam 1986). The model is

$$\frac{dP}{dt} = P(b'a'R + \beta\alpha N - m'),$$

$$\frac{dN}{dt} = N(abR - m - \alpha P), \tag{5}$$

and

$$\frac{dR}{dt} = R[r(1 - R/K) - aN - a'P].$$

Model (5) has five possible equilibria: (i) all species are at zero density; (ii) the basal resource is present at density K, but the IGpredator and IGprey are absent; (iii) the resource and IGprey are present, with respective equilibrial densities of m/ab and $(r/a)(1 - m/abK)$, but the IGpredator is absent; (iv) the resource and IGpredator equilibrate at densities, respectively, of $m'/a'b'$ and $(r/a')(1 - m'/a'b'K)$, without the IGprey; and (v) all species are present, with densities, respectively, of

$$R^* = K(r\alpha\beta + a'm\beta - am')/D,$$

$$N^* = (Kaa'bm' + m'r\alpha - Ka'^2b'm - Ka'b'r\alpha)/\alpha D,$$

and

$$P^* = (Kaa'b'm + Kabr\alpha\beta - Ka^2bm' - mr\alpha\beta)/\alpha D,$$

where

$$D = Kaa'(b\beta - b') + r\alpha\beta.$$

For given parameters, not all these equilibria exist. Moreover, the existence of certain equilibria requires that other equilibria be unstable, in that species not present can invade. Finally, equilibrium (v) may be locally unstable, in which case alternative equilibria may exist, or the system may exhibit unstable dynamics.

A positive carrying capacity for the basal resource implies equilibrium (i) is unstable. We assume this is true.

Equilibrium (ii) is stable, provided neither the IGpredator nor the IGprey can subsist on the resource alone. If so, none of the other equilibria exist, either. Equilibrium (ii) can be unstable in three distinct ways: the IGprey can invade, which requires $K > m/ab$; the IGpredator can invade, which requires $K > m'/a'b$; or both these inequalities hold, so either consumer can increase when rare and the resource is at K.

Equilibrium (iii) exists, provided the IGprey can invade at a resource density of K. Moreover, this equilibrium is stable with respect to small changes in either resource or IGprey densities (a standard result for the Lotka-Volterra predator-prey model with logistic prey growth). The condition for this equilibrium to be unstable with respect to invasion by the IGpredator is

$$a'b'(m/ab) + \alpha\beta(r/a)(1 - m/abK) - m' > 0. \tag{6}$$

If this inequality is reversed, the IGpredator is excluded from the community because of a paucity of resources (averaging over ambient levels of both the basal resource and the IGprey). Exclusion of the IGpredator when rare is likely if the IGprey is an efficient competitor that reduces the basal resource to low levels (small m/ab) and is also itself a low-quality or hard-to-catch prey item for the IGpredator (small $\alpha\beta$). An increase in the IGprey's ability to capture the basal resource (parameter a) may make invasion by an IGpredator more difficult in two distinct ways: such an increased ability reduces the abundance of the basal resource; and for sufficiently large values, increasing the attack rate decreases the equilibrial abundance of the IGprey (because of overexploitation), thereby reducing the overall food supply for the IGpredator. For any set of parameters, there is some value of the attack rate by the IGprey on the resource above which the IGpredator is excluded when rare. Conversely, increasing basal resource productivity (via r or K) eases invasion by the IGpredator.

Equilibrium (iv) exists, provided the IGpredator can invade with the basal resource at K. This equilibrium is stable to perturbations in either basal resource or IGpredator density. If this equilibrium does not exist (e.g., at low K), the IGpredator cannot subsist on just the basal resource. Condition (6) may nonetheless hold if the IGpredator garners sufficient benefit from the IGprey to persist. At low resource K, the IGpredator may be absent from the community if the IGprey is not also present.

The condition for the equilibrium with the IGpredator and basal resource to be unstable because of invasion by the IGprey is

$$ab(m'/a'b') - \alpha(r/a')(1 - m'/a'b'K) - m > 0. \tag{7}$$

If inequality (7) is reversed, the IGprey is excluded because there are insufficient resources for it to withstand the cumulative mortality imposed by the IGpredator and density-independent factors. Increasing the productivity of the basal resource (e.g., via increases in either r or K) increases the equilibrial abundance of the IGpredator, thereby making invasion by the IGprey more difficult. For any given set of trophic parameters (a, a', etc.), there is some value of r for the basal resource, above which the IGprey will be excluded by the IGpredator. In effect, the basal resource indirectly excludes the IGprey via the IGpredator's numerical response.

Finally, equilibrium (v) (all species present) exists in two distinct sets of cirumstances. First, if the quantity $D > 0$, the equilibrial densities are positive when the following inequalities hold:

(a) $R^* > 0$, if $a'm\beta + r\alpha\beta - am' > 0$;

(b) $N^* > 0$, if $m'r\alpha + Kaa'bm' - Ka'^2b'm - Ka'b'r\alpha > 0$; and

(c) $P^* > 0$, if $Kabr\alpha\beta + Kaa'b'm - Ka^2bm' - mr\alpha\beta > 0$.

Conditions (b) and (c) are equivalent to the conditions (6) and (7) for invasion by the IGprey and IGpredator, respectively. A little manipulation shows that conditions (b) and (c) also imply that $R_N^* < R_P^*$, as shown for the general resource-consumer model (2).

If $D < 0$, positivity of the full equilibrium requires that the inequality terms in conditions (a), (b), and (c) be reversed. In this case, the existence of the three-species equilibrium requires that the two alternative communities corresponding to equilibria (2) and (3) (i.e., the IGpredator and IGprey, each respectively alone with the basal resource) be noninvasible. A necessary condition for $D < 0$ is that $b\beta < b'$. For instance, the IGprey might provide a low benefit (β) to the IGpredator, relative to the basal resource. If so, D is increasingly likely to be negative at higher exploitation rates.

At high K for the basal resource, alternative states arise within a range of resource productivities, bound as follows: $(ab/\alpha)(R_P^* - R_N^*) < r < (a'ab'/\alpha\beta)$ $(R_P^* - R_N^*)$. (If these inequalities are reversed, this relation defines a range of resource productivities permitting mutual invasion by either IGprey or IGpredator at high K.) Roughly speaking, alternative, noninvasible states (with either the IGpredator or the IGprey present at equilibrium, but not both) are more likely if both the IGpredator and IGprey can effectively exploit the basal resource to a level well below K (provided the IGprey is superior), the IGprey gives little direct benefit to the IGpredator (small β), but the IGpredator inflicts significant mortality on the IGprey (high α).

To evaluate local stability of the full three-species equilibrium, we follow standard procedures (e.g., May 1974). The Jacobian matrix of model (5) is as follows:

$$\begin{bmatrix} 0 & \beta\alpha P^* & b'a'P^* \\ -\alpha N^* & 0 & baN^* \\ -a'R^* & -aR^* & -\dfrac{rR^*}{K} \end{bmatrix}.$$

The characteristic equation is $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$, where

$$a_1 = \frac{r}{K}R^*,$$

$$a_2 = a'^2b'R^*P^* + a^2bR^*N^* + \alpha^2\beta N^*P^*,$$

and

$$a_3 = \frac{\alpha R^*P^*N^*D}{K}.$$

The three-species equilibrium is locally stable if the real part of the roots of the characteristic equation are negative. The Routh-Hurwitz criteria for this to hold are given by the inequalities $a_i > 0$ ($i = 1, 2, 3$) and $a_1a_2 > a_3$. By inspection, a_1 and a_2 are both positive, and $a_3 > 0$ if and only if $D > 0$.

It follows that if the three-species equilibrium exists and $D < 0$, then the equilibrium is locally unstable. We showed earlier that $D < 0$ was the condition for the existence of alternative, noninvasible equilibria (one with just the IGpredator subsisting on the basal resource, the other with the IGprey). Numerical simulations suggest that when the system is nudged from the three-species equilibrium

and $D < 0$, it converges to one or the other of these two edge (two-species) equilibria.

If the three-species equilibrium exists and $D > 0$, then either IGpredator or IGprey can invade when rare and the other two species are at equilibrium. However, this does not guarantee biological persistence if the full system shows large fluctuations in abundance. One can readily demonstrate numerically that the full three-species equilibrium can be locally unstable (Holt 1996). Although for many parameter choices the point equilibrium is globally stable, many parameter combinations can produce a highly unstable system, even though each species can invade when rare. Such instability may emerge with even small amounts of IGP. Figure 1 provides examples of stability domains for the Lotka-Volterra IGP model. In the examples shown, $a < a' = 1$ and $b < b' = 1$; the IGpredator is less effective than the IGprey at exploiting the basal resource (a necessary condition for mutual invasibility). For parameter choices in the parameter domains denoted *stable* and *unstable,* the IGpredator and IGprey can invade systems at equilibrium with either the basal resource or the other predator at equilibrium with the resource. (The boundaries of the stability domains were determined numerically from the above stability conditions and checked with numerical integration of the full model.) Near the boundary of stable and unstable coexistence, limit cycles of small amplitude occur. Away from the boundary in the unstable region, however, the full system can show dramatic fluctuations in abundance (Holt 1996).

The algebraic conditions separating stable from unstable parameter combinations do not reduce to easily interpretable, compact forms. Several limiting cases favoring stability or instability are easily derived, however. First, if either N^* or P^* is sufficiently near 0, the equilibrium is stable. In this case, the third species in effect makes only a minor perturbation in an inherently stable pairwise interaction. Second, if $b\beta < b'$ (with $D > 0$), then the Routh-Hurwitz criteria are satisfied and the equilibrium is stable. Conversely, if R^* is depressed sufficiently low and $b\beta > b'$, then the equilibrium is unstable. Numerical examples we have observed of unstable dynamics typically have strong asymmetries in the benefits the two consumer species derive from the basal resource, with the IGpredator enjoying less benefit than the IGprey.

In the unstable domain, population fluctuations can lead to transient periods when one or more species is at very low densities, three to six orders of magnitude lower than equilibrial densities (Holt 1996). In more realistic models incorporating demographic stochasticity, this dynamic instability is likely to lead to extinctions, thus preventing the long-term coexistence of species in IGP that otherwise fit the mutual invasibility criteria.

A Model with Unusual Alternative States

In ecological models in which per capita growth rates are linear functions of the densities of the interacting species, the only feasible alternative states involves various distinct species sets (Lewontin 1969). In model (5), for example, the only alternative stable states of the system are IGpredator + basal resource and IGprey + basal resource. Introducing nonlinearities into the resource dynamics or the predation terms increases the range of possible alternative stable states
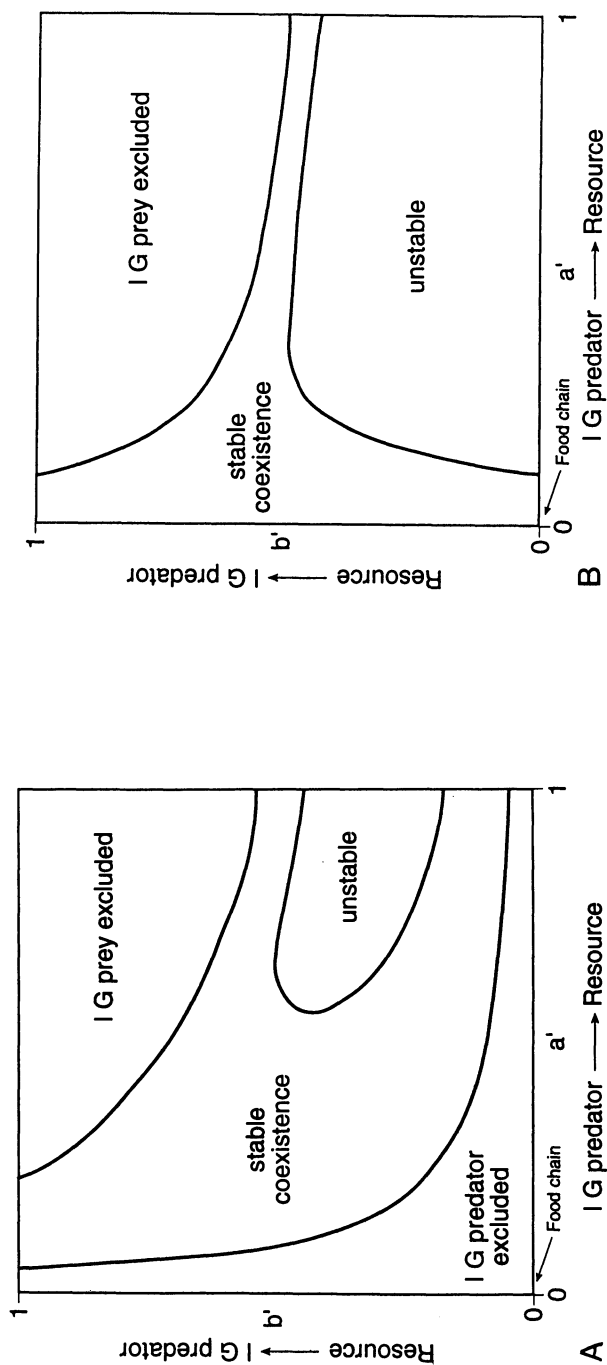
FIG. 1.—Examples of domains of stability and instability for the Lotka-Volterra IGP model. *A*, $r = 1$, $k = 1$, $a = 1$, $\alpha = 0.5$, $b = 1$, $\beta = 1$, $m = 0.5$, and $m' = 0.5$. In the zones denoted *stable coexistence* and *unstable*, both the IGpredator and IGprey can increase when rare, and the other species is at equilibrium with the basal resource. In the zone marked *unstable*, the three-species point equilibrium is unstable; numerical analyses suggest that the system exhibits large-amplitude cycles (e.g., differences of three to six orders of magnitude between peaks and lows), except very near the border between the stability regions. *B*, As in *A*, but $\alpha = 1$, $m = 0.1$, $m' = 0.5$.

and, in particular, opens up the possibility of alternative states displaying qualitatively distinct local dynamics.

To illustrate, consider the nonlinear model of exploitative competition introduced by Schoener (1974, 1976), which we modify to include IGP as follows:

$$\frac{dP}{dt} = P\left(\frac{b'e'I}{e'P + eN} + \beta\alpha N - m'\right)$$

and (8)

$$\frac{dN}{dt} = N\left(\frac{beI}{e'P + eN} - \alpha P - m\right).$$

The first terms inside the parentheses describe demographic consequences for the consumers of exploitative competition between them, and the second terms describe IGP. A mechanistic justification (Schoener 1974) for the exploitative competition term is to imagine that resources flow into the system at a constant rate I, that all resources are consumed, and that the per capita share of resources accruing to an individual of the IGpredator is $e'/(e'P + eN)$. The ratio e/e' measures the relative abilities of the two consumers to compete for the resource. In this formulation of exploitative competition, the marginal competitive effect of either species on the other diminishes with increasing density.

A necessary condition for persistence of the IGprey is that $(b/m)(e/e') > b'/m'$; if the two species are similar exploitatively, small amounts of IGP lead to exclusion of the IGprey. Rather than describe in formal detail all the conditions for coexistence and exclusion, for our current purpose it suffices to describe the interaction graphically. This model leads to hyperbolic isoclines for both species. Some examples are shown in figure 2 (modified from Polis et al. 1989). The isoclines are arranged in order of increasing resource input I (a measure of environmental productivity). The IGprey isocline has a negative slope. The isocline of the IGpredator is negative at low IGprey densities but becomes positive at higher densities, corresponding to a shift from a net competitive effect to a net predation effect. Consider the case depicted in figure 2B. The system exhibits two alternative stable states: (i) the IGpredator is present alone, with the IGprey excluded by a mixture of predation and competition, and (ii) the IGprey and IGpredator both persist, at densities at which their interaction dynamically resembles a classical predator-prey interaction. For the latter equilibrium, following small perturbations in density, the system returns to equilibrium with damped oscillations in the abundances of each species, the IGpredator lagging the IGprey. But globally, the interaction is in a broad sense a net competitive interaction, because the IGpredator is depressed in abundance (relative to its abundance when alone) by the IGprey. Whether the system becomes dominated by the IGpredator, or instead has a persistent IGpredator-IGprey interaction, is determined by initial densities.

DISCUSSION

Interest in IGP has blossomed recently, and there are now numerous excellent examples from a wide range of communities (e.g., Cortwright 1988; Purcell 1991;
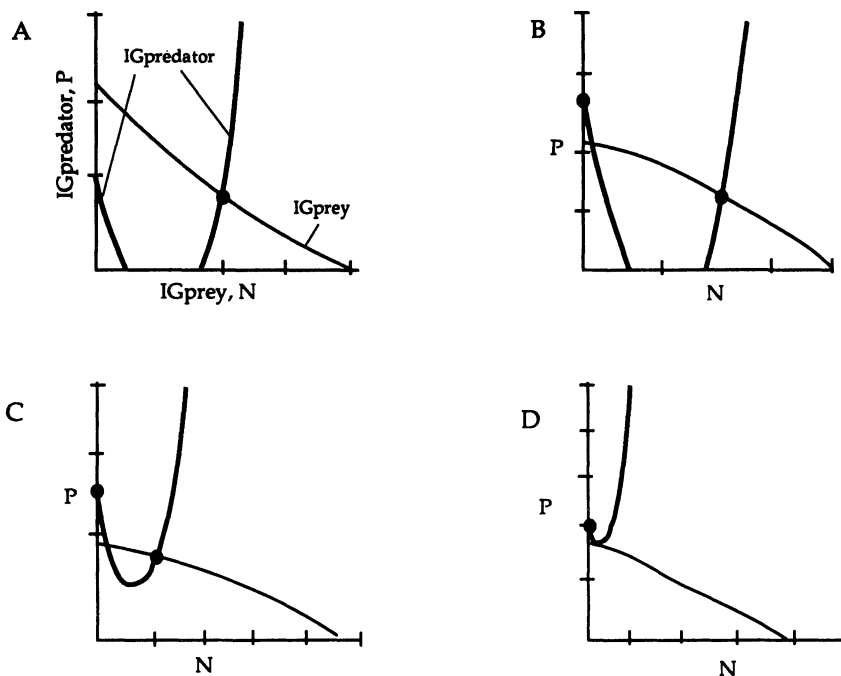
Fig. 2.—Zero-growth isoclines for the Schoener model of exploitative competition, gener-
alized to include IGP. The heavy line denotes the IGpredator isocline, which may have two
segments in the positive quadrant. The lighter line is the IGprey isocline. The predator
isocline is a hyperbolic curve, concave upward, because of the strong nonlinearity assumed
in resource exploitation. The curves from *A* to *D* are arranged in order of increasing input
of the basal resource (denoted by *I* in the text). *A*, Low productivity. There is a single
predator-prey equilibrium. *B* and *C*, Two levels of intermediate productivity. There are two
equilibrium. One is locally a predator-prey equilibrium; the other has just the IGpredator,
and the IGprey is excluded. *D*, High productivity: a single equilibrium exists, with only the
IGpredator present.

Soto and Hurlbert 1991; Spences and Carcamo 1991; Valdes Szeinfeld 1991; Don-
caster 1992; Diehl 1993, 1995; Johnsson 1993; Wissinger and McGrady 1993;
Kuris and Laferty 1994). In IGP, species pairs interact in a mix of functionally
distinct ways, making the system inherently more complex than the unidimen-
sional interactions of pure competition or predation. It is useful to stand back
from the fascinating natural history details of particular examples to discern con-
ceptual threads linking disparate systems. The models explored here are natural,
first-order extensions of standard multispecies competition and predator-prey
models, generalized to include IGP. Our results include a general criterion for
coexistence in IGP systems, an identification of circumstances leading to alterna-
tive stable equilibria, and a demonstration of the potential for unstable population
dynamics. We suggest that persistent, strong IGP raises a puzzle of species coex-
istence, particularly in productive environments.
    Intraguild predation blends the attributes of several well-studied community

modules, such as food chains, exploitative competition, and apparent competition. Some of our theoretical results parallel phenomena well known from studies of these related modules. It is thus useful to place our results into a broader context, highlighting similarities and differences among these modules.

First, the IGP module incorporates a food chain module, because energy and nutrients flow through the intermediate species to the top species. As in food chain models (e.g., Rosenzweig 1973; Hallam 1986), the productivity of the basal resource influences the ability of the top level (the IGpredator) to persist. Given that the IGprey is superior at resource exploitation, at sufficiently low K for the basal resource the IGpredator will not persist. Also, given that the IGpredator and IGprey coexist, condition (4) states that the IGpredator exerts an indirect top-down influence, increasing basal resource levels at equilibrium, compared with levels expected with just the IGprey.

However, the value of resource K at which the top predator occurs may be lowered, compared with a similar food chain, because the IGpredator can use the basal resource directly. Because of this direct effect of the IGpredator on the basal resource, the magnitude of the top-down effect on basal resource abundance may be reduced, compared with similar food chain models (R. D. Holt, unpublished results).

Second, the IGP module incorporates the module of exploitative competition (Tilman 1982), because both predators share the basal resources. The models suggest that coexistence requires that the IGprey be superior at exploiting shared resources. Species coexistence in the face of competition usually involves resource or niche partitioning (Chesson 1991) or selective predation on the superior competitor (Yodzis 1986; Holt et al. 1994). One may interpret coexistence in systems with IGP in either way. For instance, the inferior competitor persists because it itself inflicts mortality differentially on the superior competitor. Moreover, there is obviously a difference in niche, at least if the niche is defined by resource use, since the IGpredator uses a resource unavailable to the IGprey— namely, the IGprey itself. For coexistence, the inferior competitior (the IGpredator) must gain sufficiently from predation on the IGprey to offset competitive inferiority on the shared resource. Indeed, inferior competitors for resources in unproductive environments may require predation on more effective exploitative competitors to persist at all.

The intermediate species has to be a sufficiently strong competitor for the basal resource (in the sense derived for model [2]) to withstand predation from the top predator. Species roughly equal in competitive ability are unlikely to coexist, if one species preys on the other. Intraguild predation thus tends to hamper coexistence if there is symmetrical competition.

Third, the IGP module incorporates the module of apparent competition (Holt 1977, 1984; Holt and Lawton 1994), because both the basal resource and the IGprey share the top predator. In shared predation, one prey species (here, the IGprey) is vulnerable to exclusion if the the alternative prey (the basal resource) is sufficiently productive (Holt and Lawton 1994; Holt et al. 1994). Exclusion of an IGprey species in a sense reflects the combined effects of exploitative and apparent competition.

The latter effect predominates at high resource productivity. Along gradients in environmental productivity, coexistence between the IGpredator and IGprey (given that it happens at all) is most likely at intermediate levels of production. At low productivity, exploitative competition dominates, and the IGprey's superiority in resource competition determines the outcome. At high productivity, apparent competition dominates, because of the numerical response of the IGpredator. The results presented for models (5) and (8) show that at high productivities for the basal resource, IGpredators tend to be sustained at sufficiently high abundance to exclude the IGprey.

Fourth, standard Lotka-Volterra models with linear functional responses for the community modules of simple unlinked food chains, exploitative competition, and apparent competition (without direct interference) all settle to unique, stable point equilibria (Holt 1977; Tilman 1982; Hallam 1986). The blending of these modules in IGP permits alternative stable equilibria to arise. In model (6), alternative equilibria arise at intermediate productivity levels, particularly if the IGpredator does not gain substantially from consumption of IGprey. The generalized Schoener model illustrates that in IGP the net interaction pattern (including indirect effects via the resource base) may resemble either classical competitive interactions or classical predator-prey interactions, depending on the realized densities of the two species, the rate of resource renewal, and the details of the predator-prey interaction. Alternative equilibria seem particularly likely if there is a strong asymmetry in the benefit the IGpredator receives from consuming the IGprey and the mortality it inflicts on the IGprey.

Finally, the Lotka-Volterra IGP model reveals that combining these modules into IGP can generate dynamic instability, even when all pairwise interactions and constituent modules (food chains, etc.) are stable, and each species can increase deterministically when rare. This model adds to a growing list of unstable dynamics known to arise in three-species systems with no propensity for sustained oscillations in any pairwise interactions (e.g., among three competing species in a competitive network: May and Leonard 1974; a generalist predator attacking two directly competing prey: Gilpin 1979). Incorporating nonlinear functional responses into models of IGP is likely to make complex dynamics even more likely (as with food chain models: Hastings and Powell 1991; McCann and Yodzis 1995).

An intuitive interpretation of how instability arises in the Lotka-Volterra IGP model is as follows. In a food chain without IGP, following a perturbation, the system approaches equilibrium with damped oscillations, with the IGprey increasing, followed by a lag by the IGpredator. Given IGP in the same chain, the decline of the IGpredator is slowed because it has an alternative food source, the basal resource, which in turn allows it to continue to prey on the IGprey, even as the IGprey declines to low numbers. Moreover, the basal resource itself recovers less rapidly than in an unlinked food chain (because of consumption by the IGpredator). The net effect is that the IGprey gets driven to lower densities, and recovers more slowly, than expected in a food chain without IGP. The IGprey begins to rebound in numbers only when the IGpredator has sufficiently declined.

When it does so, the IGprey can grow rapidly, because the resource by then has had sufficient time to increase greatly. The overall effect is that the IGprey experiences pulses of rapid growth, followed by long periods of low densities because of sustained predation. Such instability compounds the problem of sustained coexistence in systems with strong IGP.

Future Directions

The results described here highlight a puzzle in species coexistence: systems with strong IGP are prone to species exclusion, particularly in productive environments. Yet as noted earlier, such systems are common in natural communities. As with the puzzle of coexistence raised by exploitative competition for limiting resources, one profitable avenue for work should be to ascertain mechanisms for coexistence in systems with strong IGP. The results presented here are starting points, not a conclusive theoretical overview of all the potential ramifications of IGP, but they do provide useful yardsticks for gauging potential mechanisms for coexistence. Rather than attempt to cover the entire spectrum of reasonable modifications (e.g., nonlinear functional responses, temporal variability, direct interference), we touch on recurrent features of empirical IGP systems revealed in recent reviews (Polis et al. 1989; Diehl 1993) not incorporated into the above models.

Age or Stage Structure Complications

The predatory interaction in many IGP systems is restricted to particular ages or stages (e.g., Polis 1988; Wilbur 1988; Wissinger 1992; others cited in Ebenman and Persson 1988). Age- or stage-restricted predation is known to have complicated effects in ordinary predator-prey interactions (e.g., Hastings 1983), so it is reasonable to expect a range of interesting complications arising in IGP systems also. For instance, age-restricted predation may provide a partial escape from predation for the IGprey, which can be stabilizing. Moreover, different ages or stages often use distinct resources and are exposed to distinct suites of natural enemies (Polis 1994); this niche differentiation is likely to reduce the likelihood of exclusion because of competition for shared resources.

Adaptive Behaviors in Both Prey and Predator

The above models all assume very simple behaviors. There is growing appreciation of the complications in standard predator-prey interactions that may arise if either predators or prey modify their behaviors adaptively (e.g., Holt 1983; Abrams 1987, 1993). Adaptive behaviors may facilitate coexistence in IGP.

For instance, if adaptive foraging by the IGpredator leads to switching (sensu Murdoch and Oaten 1975) between the basal resource and the IGprey, it is likely that the entire interaction could be stabilized, and alternative stable states entirely missing the IGprey should be unlikely. Recall that a necessary condition for the existence of alternative states in IGP systems is that the IGprey is superior at resource exploitation (otherwise, the IGpredator simply excludes the IGprey). Assume that this is the case. If the IGpredator switches, ignoring rarer prey, the

IGprey when rare will not be exposed to predation. Yet it will experience an ambient level of resources set by the (exploitatively inferior) resident IGpredator and so should be able to increase in numbers. Thus, an IGprey that is a superior competitor should coexist with a switching IGpredator. In like manner, adaptive antipredator behaviors by the IGprey could foster its persistence. Behavioral modifications reducing predation experienced by the IGprey might include altered foraging modes (e.g., speed of movement during resource acquisition) or shifts in the temporal or spatial arenas of foraging (Lima and Dill 1990).

Spatial Heterogeneity

The models analyzed here are all "closed," with no migration dynamics. It is well known that in a patchy environment, predators and prey may persist by colonization-extinction dynamics, even though each local interaction is unstable. Such spatial effects may at times facilitate coexistence of IGpredator and IGprey. However, if the IGpredator can sufficiently rapidly colonize patches with the basal resource but without the IGprey, the net effect may well be to hamper persistence by the latter. Conversely, if the IGprey has absolute refuges from predation, then the chances of exclusion are greatly reduced and alternative stable states (at least without the IGprey) become less likely. Diehl (1983) notes that many examples of strong IGP do seem to involve spatial refuges for the IGprey.

Additional Species

Most IGP systems are embedded in speciose food webs; other species can have a significant effect on the dynamics of the interacting triad of a basal resource, IGprey, and IGpredator. Two straightforward consequences of additional species are that providing exclusive resources for the IGprey should make it more difficult for it to be excluded by the IGpredator, even if the IGprey is inferior at exploiting the shared resource, and providing additional nonshared resources for the IGpredator makes the IGprey more vulnerable to exclusion via the IGpredator's numerical response (Holt 1984), but less vulnerable to exclusion if the IGpredator does not show a strong numerical response but instead can be individually satiated or switches (Holt 1996).

CONCLUSIONS

Intraguild predation may confound simple expectations for manipulative experiments in community ecology. For instance, predator removal may lead to an unexpected decline in a particular prey species, because an unmonitored intermediate predator increased in abundance. Several examples of this phenomenon have now been observed (e.g., Ambrose 1984; Pacala and Roughgarden 1984; Sih et al. 1985; Hurd and Eisenberg 1990; Ehler 1992; Wissinger and McGrady 1993; also see Polis and Holt 1992). Or removing one competitor may lead to an unexpected reduction in another competitor, because the latter was actually consuming the former, and the IGprey was a significant dietary item for the IGpredator (see, e.g., Hairston 1986).

In community ecology, a perpetual tension exists between the need to seek simple, unifying principles and the desire to address the manifest complexity of ecological communities. Intraguild predation is often a major determinant of the distribution and abundance of interacting species and warrants concerted theoretical and empirical attention. In this article, we have elucidated some general principles of coexistence in simple IGP systems and demonstrated that such systems are capable of a wide range of alternative states and complex dynamic behaviors. We have also sketched how our conclusions might need to be tempered, given various realistic complications (e.g., alternative prey). We believe that the close analysis of community modules—such as three-species IGP—provides a useful bridge between the thoroughly analyzed dynamics of pairwise species interactions and the richly complex multispecies world we all hope in the end to understand.

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