The Effects of Enrichment on the Dynamics of Apparent Competitive Interactions in Stage-Structured Systems

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abstract: In the absence of other limiting factors, assemblages in which species share a common, effective natural enemy are not expected to persist. Although a variety of mechanisms have been postulated to explain the coexistence of species that share natural enemies, the role of productivity gradients has not been explored in detail. Here, we examine how enrichment can affect the outcome of apparent competition. We develop a structured resource/consumer/natural enemy model in which the prey are exposed to attacks during a vulnerable life phase, the length of which depends on resource availability. With a single prey species, the model exhibits the "paradox of enrichment," with unstable dynamics at high levels of resource productivity. We extend this model to consider two prey species linked by a shared predator, each with their own distinct resource base. We derive invasion and stability conditions and examine how enrichment influences prey species exclusion and coexistence. Contrary to expectations from simpler, prey-dependent models, apparent competition is not necessarily strong at high productivity, and prey species coexistence may thus be more likely in enriched environments. Further, the coexistence of apparent competitors may be facilitated by unstable dynamics. These results contrast with the standard theory that apparent competition in productive environments leads to nonpersistent interactions and that coexistence of multispecies interactions is more likely under equilibrial conditions.

Keywords: age structure, coexistence, equivalence, indirect interactions, invasion, predator-prey dynamics.

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The effect of productivity on community structure and ecosystem functioning is a central theme in ecology (DeAngelis 1992). Theoretical studies have highlighted, for instance, how the impact of competition can be modulated by the availability of nutrients (Riebesell 1974; Tilman 1982; Huston and DeAngelis 1994) and how food web structure and dynamics can be affected by nutrient supply and enrichment (DeAngelis et al. 1989; Leibold 1989; Morin 1999). Many studies on productivity and enrichment have examined how changes in the basal resource affect the relative abundance of organisms at different trophic levels (Rosenzweig 1971; Oksanen et al. 1981; Abrams 1993). For instance, Oksanen et al. (1981; see also Oksanen and Oksanen 2000) hypothesized that predation should be more important in herbivore regulation as productivity increases. Moreover, communities show a wide range of relationships between productivity and species richness within trophic levels (Tilman 1982; Waide et al. 1999).

More recently, the population dynamic consequences of enrichment have been thoroughly developed. Initially, most work focused on pairwise interactions. Stemming from Rosenzweig's (1971) original work on the "paradox of enrichment" of predator-prey interactions, one dynamical prediction in many models is that increasing productivity can destabilize species interactions (Reibesell 1974) and increase the amplitude of predator-prey cycles (Gilpin 1975). A variety of factors correlated with increased productivity, such as increased prey growth rate and decreased prey density dependence, can increase cycle amplitude (May 1973; Yodzis and Innes 1992), and these act to restrict the persistence of the predator-prey interaction. The dynamical implications of the role of productivity gradients on more complex multispecies interactions have just begun to be explored, for instance, by the examination of how enrichment may affect subsets (modules) of food webs, such as trophic chains and competitive interactions coupled with predation and omnivory (Leibold 1989, 1996; Abrams and Roth 1994a, 1994b; Holt et al. 1994; Holt and Polis 1997; Nisbet et al. 1998; Abrams 1999; Diehl and Feiβel 2000). Our broad objective here is to develop

this theme and examine the population dynamical consequences of increasing productivity on indirect interactions between prey species.

One indirect interaction that has attracted recent interest is apparent competition. Apparent competition is defined as a $(-, -)$ interaction between two (or more) prey species that do not compete for resources but share a common natural enemy (Holt 1977, 1984, 1997a). In the absence of other limiting factors (e.g., negligible direct density dependence or resource limitation), apparent competition tends to lead to the loss of one prey species. This occurs due to the numerical response of the natural enemy. By introducing a second prey species into an established predator-prey interaction, an increase in the numerical abundance of the predators occurs. In the long run, more predators mean more attacks, and over time, the more vulnerable prey (i.e., the one that suffers higher attack rates or has the lower growth rate) is excluded (Holt and Lawton 1994). Empirical work has demonstrated how shared enemy effects are important in structuring plant-herbivore, predator-prey, and host-disease assemblages (Settle and Wilson 1990; Grosholz 1992; Bonsall and Hassell 1997, 1998; Chaneton and Bonsall 2000; Morris et al. 2001). Theoretical work on the population dynamic effects of apparent competition has shown how different factors such as fixed-number refuges (Holt and Lawton 1993, 1994), metapopulation structures (Holt 1997b; Bonsall and Hassell 2000), and the detailed functional form of predator behaviors (Holt and Lawton 1993; Bonsall and Hassell 1999; Bonsall 2003) can affect the persistence of these multispecies predator-prey interactions.

Most work on apparent competition has taken what we might call a Hutchinsonian perspective, where one seeks sets of environmental conditions that permit each species to increase deterministically when rare (which in turn requires niche partitioning). There has been in recent years a growing interest in alternative models of community organization, which pertains to situations in which species are competitively equivalent (Bell 2000; Hubbell 2001). In this case, even though there is no long-term deterministic coexistence, species may co-occur for very long transient phases before exclusion occurs. For example, in a metacommunity context, an assemblage of species may persist because each species is superior in just a few local sites, permitting co-occurrence in many sites where they are competitively equivalent. One role of theory is to help identify circumstances where competitive equivalence (and hence nonequilibrial perspectives, such as long-term transient coexistence) may be observed. In this article, we will argue that enrichment can lead to the effective equivalence of prey species sharing a common natural enemy.

Prior work has only just begun to address the impacts of enrichment on apparent competition. A model was briefly considered (Holt 1977) in which a strictly food-limited predator with a linear functional response consumed two prey species, each growing logistically without any direct or exploitative competition. If enrichment increases the carrying capacity of each prey, then coexistence typically becomes more difficult. In simple models, this effect holds in unstable as well as stable interactions (Holt and Lawton 1993; Holt 1997b). A qualitative model was further considered (Holt 1997b) in which the predator has a saturating functional response and direct density dependence. It was argued that apparent competition might be strongest at intermediate levels of productivity, because at high levels of productivity the predator numerical response will be constrained, leading to indirect mutualism via shared functional responses. However, a detailed treatment of the effects of productivity on shared enemy interactions is so far lacking in the literature.

In this article, we investigate the role of enrichment in shared enemy interactions. The approach explored here examines the interaction between two consumer species that feed on different resources but share a common natural enemy. Most existing theory on apparent competition (indeed, the bulk of predator-prey theory in general) has assumed a rather simple structure for the life history of prey species. It is typically assumed that resources enter via a birth term and that predation acts via a death term, so that formally the role of resources and predation are "separable" components of population growth. By contrast, in the structured models we consider here, resource availability determines the rate of development of individuals and consequently how long they remain susceptible to attack by the natural enemy during a vulnerable life-history stage. Prey reproduction occurs during an invulnerable stage, which provides a kind of labile, life-history refuge. Hence, enrichment directly influences the overall magnitude of predator attacks, leading to an intimate coupling between the determinants of birth and death rates that is absent in the typical prey-dependent predator-prey model.

We begin by briefly presenting the model for single resource/consumer/natural enemy interaction. This provides the basis for then investigating the role of enrichment on the invasion and dynamics of apparent competitors. We show how enrichment can affect the conditions for invasion and the consequences these effects have on the stability, instability, and mean neutrality of multispecies interactions. We will show that, under certain circumstances, competitive equivalence, and thus long-term (if not infinite) species coexistence, is likely at high levels of resource productivity, whereas at intermediate levels of resource supply, species may be rapidly excluded through the effects of apparent competition. In the discussion, we place our results into the context of recent developments
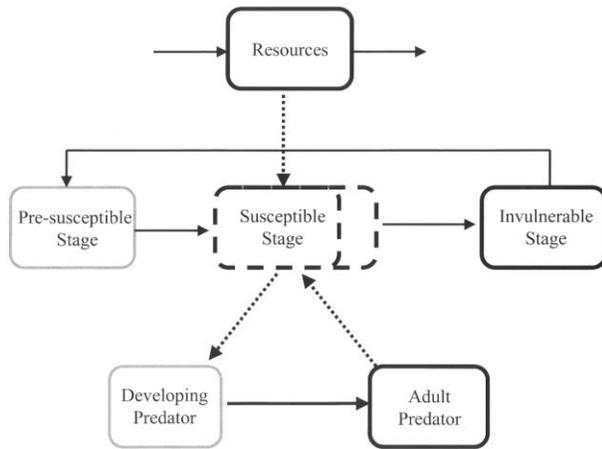
Figure 1: Schematic diagram of the resource/consumer/natural enemy system. The interaction is described by four equations that account for changes in the resource, the susceptible consumer, invulnerable consumer, and adult predator populations. The presusceptible consumer and developing predator stages (*light gray boxes*) are described by time delays in the susceptible consumer (*bold boxes*) and adult predator (*bold boxes*) equations, respectively. The resources affect the consumers by determining the length of the juvenile consumer class. The juvenile consumer stage is also susceptible to attack by the natural enemy. Solid arrows represent life-history transitions, dashed arrows trophic interactions.

regarding the role of productivity on the coexistence and dynamics of multispecies assemblages.

Resource/Consumer/Natural Enemy Model

As noted, the motivation behind this study is to understand how resource enrichment affects the patterns and persistence of indirect interactions between prey that share a common natural enemy. We assume that the interaction is stylized in the form of an insect prey-predator (or parasitic wasp) interaction. The consumer populations are structured into two age classes: a vulnerable (larval) stage and an invulnerable (adult) stage. The vulnerable consumer stage is susceptible to attack by the natural enemy for a variable period of time. This period of susceptibility is driven by how much resource can be converted into growth, and so susceptibility of attack changes with resource availability (and indirectly with vulnerable consumer population size). Our model builds directly on the structured population models developed by Gurney and Nisbet (Gurney et al. 1983; Nisbet and Gurney 1983). We assume that adult survival and fecundity are independent of resource availability. Similarly, the predator population is structured into two age classes, a juvenile stage and an adult stage; predator reproduction depends upon the availability of vulnerable consumers. Similar single predator-

prey age-structured models with fixed juvenile developmental times have been analyzed by Murdoch et al. (1987, 1997), Godfray and Hassell (1989), and Gordon et al. (1991). In general, the length of the invulnerable prey stage influences the stability of the interaction; differences in the ratio of predator-to-prey development times lead to limit cycles and, in particular, to generation cycle dynamics.

The general model developed here is a resource/consumer/natural enemy interaction in which the feeding response by the consumer has a direct, dynamical effect on the time that the consumer is susceptible to attack by the natural enemy (fig. 1). This contrasts with standard predator-prey models, such as Lotka-Volterra models, where the consumer feeding rate has a direct effect on prey births but no direct effect on deaths due to predatory attacks. The predator-prey interaction can be formulated as a set of delay-differential equations that describe in turn the dynamics of the resource, the dynamics of the consumer population, and the dynamics of the natural enemy population. First, the dynamics of the resource (R) can be represented as follows:

$$\frac{dR}{dt} = \lambda - f(R) \times L_{(t)} - \mu \times R_{(t)}. \tag{1}$$

Here, λ is the resource supply rate, $f(R)$ is the feeding response of the vulnerable consumer class (of density $L_{(t)}$ at time t) on the resource (R), and μ is the depletion rate of the resource. Changes in resource occur simply through gains due to resource supply (λ) and losses due to consumer feeding ($f(R) \times L_{(t)}$) and depletion ($\mu \times R_{(t)}$). The model is most appropriate to abiotic or detrital resources, whose recruitment does not depend on resource abundance. Enrichment of an environment may occur by either an increase in resource supply rate (λ) or a decrease in abiotic depletion rate (μ).

Second, the dynamics of the susceptible (larval; L) and invulnerable (adult; A) consumer classes can be represented as follows:

$$\frac{dL}{dt} = r_{A} \times A_{(t-\tau E)} \times \sigma_{E} - g(P) \times L_{(t)}$$
$$- d_{L} \times L_{(t)} - M_{L(t)}, \tag{2}$$

$$\frac{dA}{dt} = M_{L(t)} - d_{A} \times A_{(t)}. \tag{3}$$

Here, r_{A} is the reproductive rate of the invulnerable consumer class (A) at time $t - \tau E$, σ_{E} is the survival through the presusceptible (egg) stage (of length τE), $g(P)$ is the per capita mortality due to predation, and d_{L} and d_{A} are

the density-independent mortalities for the vulnerable and invulnerable consumer stages, respectively. The maturation of vulnerable consumer to the invulnerable class $M_{L(t)}$ is given as

$$M_{L(t)} = r_A \times A_{(t-\tau E-\tau L)} \times \sigma_E$$

$$\times \; e^{-\int_{t-\tau L}^{t}[g(P)+d_L] \times dx} \times \frac{f(R_{(t)})}{f(R_{(t-\tau L)})}. \tag{4}$$

When $t > \tau L$, the maturation term is the product of the number of individuals entering the presusceptible stage (at time $t - \tau E - \tau L$), surviving through to the end of the vulnerable consumer stage (a variable τL time units), and the vulnerable consumer development rate (which is determined by the resource acquisition rate $f(R_{(t)})$). When $t < \tau L$, maturation is of the initial juvenile population (at time $t = 0$) and is a function of mass gain and survival through the stage (Nisbet and Gurney 1983; Nisbet 1997). The time spent in the susceptible consumer stage can be found by equating mass gain (m) for the susceptible consumer stage to the integral of feeding rate over the interval $t - \tau L$ to t:

$$m = \int_{t-\tau L}^{t} f(R) \times dx. \tag{5}$$

Differentiating this integral with respect to time allows the time lag (τL) to be expressed as a dynamic variable (Nisbet and Gurney 1983):

$$\frac{d\tau L}{dt} = 1 - \frac{f(R_{(t)})}{f(R_{(t-\tau L)})}. \tag{6}$$

This variable time delay formulation (Nisbet and Gurney 1983) allows the dynamics of resource availability on consumer development to be succinctly described and captures the observation that in many organisms a fixed amount of mass must be acquired before successful maturation to the next age class can occur (Dyar 1890; Wigglesworth 1965). Finally, the dynamics of the natural enemy can be represented by

$$\frac{dP}{dt} = -d_P \times P_{(t)} + g(P_{(t-\tau JP)}) \times L_{(t-\tau JP)} \times \sigma_{JP}. \tag{7}$$

Here, d_P is the stage specific mortality of the adult predators, σ_{JP} is the survival through the juvenile natural enemy stage, and τJP is the length of the juvenile natural enemy stage. Changes in adult predator numbers occur through gains due to predation of vulnerable consumers ($g(P_{(t-\tau JP)}) \times L_{(t-\tau JP)} \times \sigma_{JP}$) and losses due to density-

independent mortality events ($d_P \times P_{(t)}$). The above model describes interactions between a single prey species and a predator in the context of resource exploitation by the prey. Since our focus in this study is on the effects of resource enrichment on apparent competition, we confine analysis of the simpler resource-consumer and resource/consumer/natural enemy interactions to appendixes A and B, respectively, in the online edition of the *American Naturalist.*

Apparent Competition Model

To explore the role of productivity on indirect interactions between prey species, we now extend the single resource/consumer/natural enemy model to include an additional resource and consumer. The model retains the feature that the feeding response by each consumer species has a direct, dynamical effect on the time the consumer is susceptible to attack by the natural enemy. Recall that because our focus is on apparent competition, we are assuming no direct or exploitative competition between the prey, so that each has its own distinct resource base. An indirect interaction arises because the two consumers feed on exclusive resources but share a common natural enemy. The equations for the resource-consumer interaction can be described as follows:

$$\frac{dR_i}{dt} = \lambda_i - f(R_i) \times L_{i(t)} - \mu \times R_{i(t)}, \tag{8}$$

$$\frac{dL_i}{dt} = r_{Ai} \times A_{i(t-\tau Ei)} \times \sigma_{Ei} - g(P) \times L_{i(t)} - d_{Li}$$

$$\times \; L_{i(t)} - M_{Li(t)}, \tag{9}$$

$$\frac{dA_i}{dt} = M_{Li} - d_{Ai} \times A_{i(t)}, \tag{10}$$

$$\frac{d\tau Li}{dt} = 1 - \frac{f(R_{i(t)})}{f(R_{i(t-\tau Li)})}, \tag{11}$$

where

$$M_{Li} = r_{Ai} \times A_{i(t-\tau Ei-\tau Li)} \times \sigma_{Ei}$$

$$\times \; e^{-\int_{t-\tau Li}^{t}[g(P)+d_{Li}] \times dx} \times \frac{f(R_{i(t)})}{f(R_{i(t-\tau Li)})} \tag{12}$$

and $i = 1, 2$. Changes in the natural enemy population are described by

$$\frac{dP}{dt} = -d_P \times P_{(t)} + \sum_{i=1}^{2} g(P_{(t-\tau JPi)}) \times L_{i(t-\tau JPi)} \times \sigma_{JPi}. \tag{13}$$

Natural enemy numbers increase through predation on the two different consumers ($\sum_{i=1}^{2} g(P_{(t-\tau Pi)}) \times L_{i(t-\tau JPi)} \times \sigma_{JPi}$) and decline simply through density-independent mortality events ($d_P \times P_{(t)}$). Equation (13) implies that the alternative prey types are substitutable resources for the predator. For simplicity, we assume (for the most part) that the prey species subsist on resources with equivalent renewal and depletion rates.

Invasion

In this section, we evaluate two approaches for coexistence under apparent competition. We evaluate traditional criteria for deterministic coexistence, and then we consider the potential for long-term transient coexistence in terms of species equivalence.

Deterministic coexistence occurs if each of the two single resource/consumer/natural enemy interactions can be invaded by the other consumer species. A species can only invade if it has a positive growth rate when rare. Consider a simpler version of the full model described above, in which we assume that the resource for each species is fixed at a constant level R_i^*, which in turn fixes the developmental lag, and the system is at equilibrium with just one consumer and the predator. At this equilibrium, the predator density has the value given in appendix B (eq. [B4]). For the second consumer species to invade into this equilibrium requires that $dA_2/dt > 0$ (the dynamics of the juvenile component of the population are embedded in the determinants of the maturation rate, M_{Li}). It is evident that this will occur if

$$M_{L2} - d_{A2} \times A_{2(t)} > 0, \qquad (14)$$

or, more explicitly,

$$r_{A2} \times A_{2(t-\tau E2-\tau L2)} \times \sigma_{E2} \times e^{-\int_{t-\tau L2}^{t}[g(P_1^*)+d_{L2}] \times dx}$$

$$\times \frac{f(R_{2(t)})}{f(R_{2(t-\tau L2)})} - d_{A2} \times A_{2(t)} > 0, \qquad (15)$$

where P_1^* is the equilibrium density of the natural enemy in the presence of only consumer 1. If we further assume that the predator has a linear functional response to each prey species, so that $g(P) = \beta_i \times P$ (and $\mu_i \to 0$), the condition for the invasion of consumer species 2 is

$$\tau L2 < \frac{\ln\left(\dfrac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right)}{(\beta_2 \times P_1^* + d_{L2})}. \qquad (16)$$

More explicitly, this invasion criteria can be expressed as

$$\tau L2 < \frac{\ln\left(\dfrac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right)}{\lambda_1 \times \dfrac{\beta_2 \times \sigma_{JP1}}{m_1 \times d_P} \times \ln\left(\dfrac{r_{A1} \times \sigma_{E1}}{d_{A1}}\right) - \dfrac{\beta_2 \times d_{L1}}{\beta_1} + d_{L2}}. \qquad (17)$$

Under these conditions, it is expected that consumer species 2 can always invade as $\tau L2 \to 0$. However, if $\mu_2 > 0$, then $R_2^* = \lambda_2/\mu_2$ and $\tau L2^* = (m_2 \times \mu_2)/(\alpha_2 \times \lambda_2)$; the invasion condition for consumer species 2 is now

$$\frac{m_2 \times \mu_2}{\alpha_2 \times \lambda_2} <$$

$$\frac{\ln\left(\dfrac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right)}{\lambda_1 \times \dfrac{\beta_2 \times \sigma_{JP1}}{m_1 \times d_P} \times \ln\left(\dfrac{r_{A1} \times \sigma_{E1}}{d_{A1}}\right) - \dfrac{\beta_2 \times d_{L1}}{\beta_1} + d_{L2}}. \qquad (18)$$

Similarly, the first consumer will invade in the presence of the second consumer only if

$$r_{A1} \times A_{1(t-\tau E1-\tau L1)} \times \sigma_{E1} \times e^{-\int_{t-\tau L1}^{t}[g(P_2^*)+d_{L1}] \times dx}$$

$$\times \frac{f(R_{1(t)})}{f(R_{1(t-\tau L1)})} - d_{A1} \times A_{1(t)} > 0, \qquad (19)$$

where P_2^* is the equilibrium density of the natural enemy in the presence of consumer 2 alone. The invasion criteria for consumer 1 into an established interaction between the consumer 2 and the natural enemy is then

$$\frac{m_1 \times \mu_1}{\alpha_1 \times \lambda_1} <$$

$$\frac{\ln\left(\dfrac{r_{A1} \times \sigma_{E1}}{d_{A1}}\right)}{\lambda_2 \times \dfrac{\beta_1 \times \sigma_{JP2}}{m_2 \times d_P} \times \ln\left(\dfrac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right) - \dfrac{\beta_1 \times d_{L2}}{\beta_2} + d_{L1}}. \qquad (20)$$

If $d_{L1}/\beta_1 = d_{L2}/\beta_2$, then mutual invasion criteria can be explicitly derived. For consumer species 2 to invade consumer species 1, the invasion condition is

$$\frac{\lambda_2 \times \alpha_2 \times \ln\left(\frac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right)}{\beta_2 \times m_2 \times \mu_2} > \frac{\lambda_1 \times \sigma_{JP1}}{m_1 \times d_P} \times \ln\left(\frac{r_{A1} \times \sigma_{E1}}{d_{A1}}\right),$$

(21)

while the invasion of consumer species 1 into an established interaction between consumer species 2 and the natural enemy requires

$$\frac{\lambda_1 \times \alpha_1 \times \ln\left(\frac{r_{A1} \times \sigma_{E1}}{d_{A1}}\right)}{\beta_1 \times m_1 \times \mu_1} > \frac{\lambda_2 \times \sigma_{JP2}}{m_2 \times d_P} \times \ln\left(\frac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right).$$

(22)

Resource productivity enters these invasion criteria in several distinct ways. Increasing resource productivity for each species separately (λ_1 or λ_2) makes it more likely that invasion of the respective species (1 or 2) will be successful, while invasion of the heterospecific will be less likely. High productivity leads to high resource availability for the invader, and this in turn reduces the time required for development. However, predator abundance tends to be enhanced indirectly when prey development rates of the resident prey species are short (see app. B), which decreases the right-hand side of the above inequalities, thus making invasion harder. For successful invasion, the development time of the invader must be sufficiently short to outweigh the losses due to predation and mortality.

For coexistence to occur, both species must be able to increase when rare. If resource supply rates are fixed (at $\lambda \equiv \lambda_1 = \lambda_2$), the only limiting factor in the system for each prey is the abundance of their shared predator. If $d_{L1}/\beta_1 \neq d_{L2}/\beta_2$, the condition for consumer species 2 to invade is now

$$\frac{m_2 \times \mu_2}{\alpha_2} < \frac{\ln\left(\frac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right)}{\frac{\beta_2 \times \sigma_{JP1}}{m_1 \times d_P} \times \ln\left(\frac{r_{A1} \times \sigma_{E1}}{d_{A1}}\right) + \frac{\left(d_{L2} - \frac{\beta_2 \times d_{L1}}{\beta_1}\right)}{\lambda}},$$

(23)

while the conditions for species 1 to invade are

$$\frac{m_1 \times \mu_1}{\alpha_1} < \frac{\ln\left(\frac{r_{A1} \times \sigma_{E1}}{d_{A1}}\right)}{\frac{\beta_1 \times \sigma_{JP2}}{m_2 \times d_P} \times \ln\left(\frac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right) + \frac{\left(d_{L1} - \frac{\beta_1 \times d_{L2}}{\beta_2}\right)}{\lambda}}.$$

(24)

The effects of increasing productivity (λ) for the invasion of species 2 depends on the sign of $d_{L2} - (\beta_2 \times d_{L1})/\beta_1$. If $\beta_1 = \beta_2$, then $d_{L1} > d_{L2}$, and an increase in λ makes invasion more likely. However, these two invasion criteria are not likely to be met simultaneously; there will be some level of predators that can be tolerated by one prey species that is too high to be tolerated by the other. This is a version of the "P^*-rule" of dominance in simple models of apparent competition (Holt et al. 1994; Holt 1997*a*). Figure 2 shows some numerical examples of conditions for invasion; in these examples, species 2 invades (and deterministically, ultimately displaces species 1) for points below the gray line. In figure 2*A*, the invader has a growth advantage, and for equal development times, this species is able to win out in apparent competition. In figure 2*B*, the invader suffers increased density-independent mortality ($d_L = 0.75$) and only wins out if the resident has longer development times. Note that when the resource available (R_i^*) to each species is large, development time will be short, in which case the two species will be nearly equivalent with respect to invasion.

Now we assume that resources are exploited and can be depressed in abundance, and reduced resources lengthen development times. Consider, for instance, condition (16) for species 2 invading a community in which prey species 1 and the predator are at equilibrium. If resources can vary, in the absence of prey 2, its required resource is likely to be abundant, and hence $\tau L2$ will be reduced. This makes condition (16) easier to satisfy. In turn, when species 2 is resident, it will have a higher $\tau L2$; this in turn makes condition (20) easier to satisfy, permitting species 1 to increase when rare. Thus, variable development times can have profound effects on the outcome of apparent competition. In the limit of high resource levels, development times are very short, and apparent competitive exclusion is not likely to occur quickly, since few prey are exposed to predation. Variable development times can thus facilitate prey coexistence.

To return to the theme of enrichment, we again consider the invasion of consumer species 2, assuming a Type II feeding response for each consumer on its own resource.
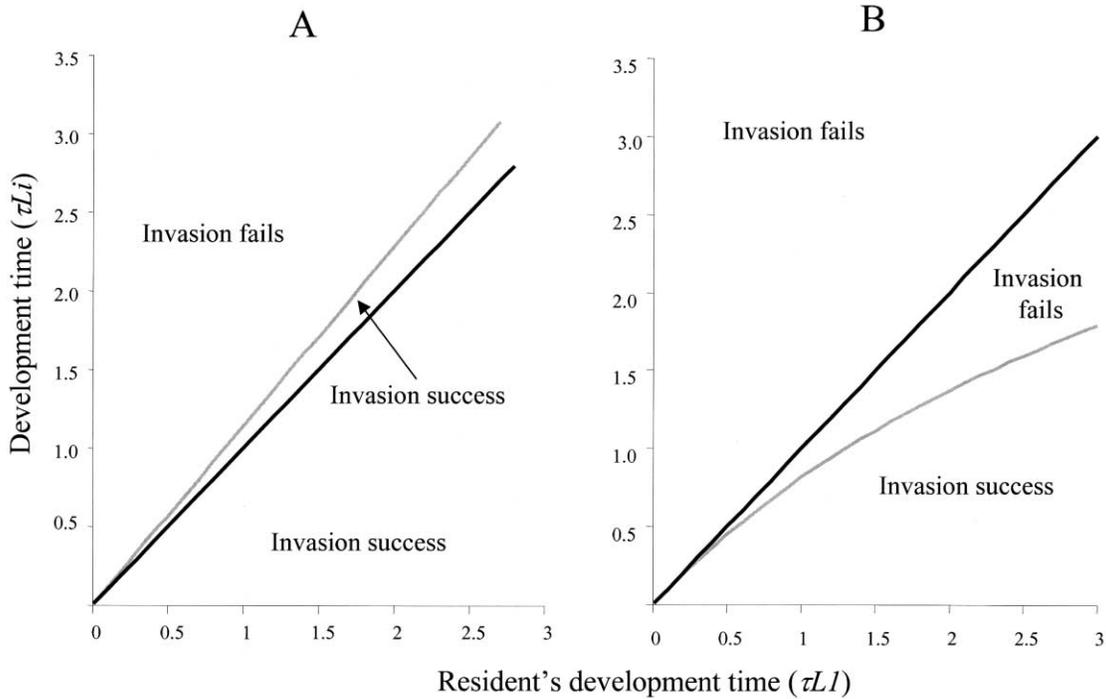
Figure 2: Invasion boundaries (*gray line*) with respect to the resident strategy (*black line*) for the invasion of a second consumer into an established resource/consumer/natural enemy interaction under a Type I feeding response by vulnerable consumers ($r_{A2} = 6.0, d_{L2} = 0.0$) and a Type I predation risk. Invasion occurs for parameter values below the gray line. *A*, Invader has a growth rate advantage. *B*, Invader suffers increased density-independent mortality ($r_{A2} = 6.0, d_{L2} = 0.75$). Other parameters: $r_{A1} = 3.0$, $\mu = 0.0$, $\beta_1 = \beta_2 = 0.1$, $a_1 = a_2 = 0.1$, $b_1 = b_2 = 0.0001$, $d_{A1} = d_{A2} = 1.0$, $d_{L1} = 0.0$, $d_P = 1.0$, $\tau E1 = \tau E2 = 1.0$, $\sigma_{E1} = \sigma_{E2} = 1.0$, $\tau JP = 1.0$, and $\sigma_{JP1} = \sigma_{JP2} = 1.0$.

The assumption of a saturating functional response means that there is a minimum value for τLi, even when resources are unlimited. We assume that the feeding rate of the vulnerable consumer class is given by $f(R_i) = (a \times R_i)/(1 + b \times R_i)$, and consequently, the integral relationship for mass gain for each species ($i = 1, 2$) is of the form

$$m_i = \int_{t-\tau Li}^{t} \frac{a \times R_i}{1 + b \times R_i} \times dx. \quad (25)$$

In the absence of the second resource-consumer interaction and negligible resource depletion ($\mu \to 0$), the following equilibria can be obtained:

$$R_1^* = \frac{\lambda}{(a \times L_1^* - \lambda \times b)}, \quad (26)$$

$$L_1^* = \frac{d_P}{\beta_1 \times \sigma_{JP1}}, \quad (27)$$

$$A_1^* = \frac{L^* \times [g(P_1^*) + d_{L1}]}{[r_{A1} \times \sigma_E - d_{A1}]}, \quad (28)$$

$$P_1^* = \frac{\ln\left(\dfrac{r_{A1} \times \sigma_{E1}}{d_{A1}}\right) - d_{L1} \times \tau L1^*}{\beta_1 \times \tau L1^*}, \quad (29)$$

$$\tau L1^* = \frac{m_1}{a} \times \left(\frac{1}{R_1^*} + b\right). \quad (30)$$

In essence, the invasion criteria for a second consumer invading an established resource/consumer/natural enemy interaction remain unchanged, except that now P_1^* is a more complex expression (because $\tau L1^*$ accounts for the effects of the Type II larval feeding response):

$$\tau L2 < \frac{\ln\left(\dfrac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right)}{(\beta_2 \times P_1^* + d_{L2})}. \quad (31)$$

In low productivity situations, species coexistence is possible because predation is relatively unimportant. In highly enriched environments, species coexistence is pos-
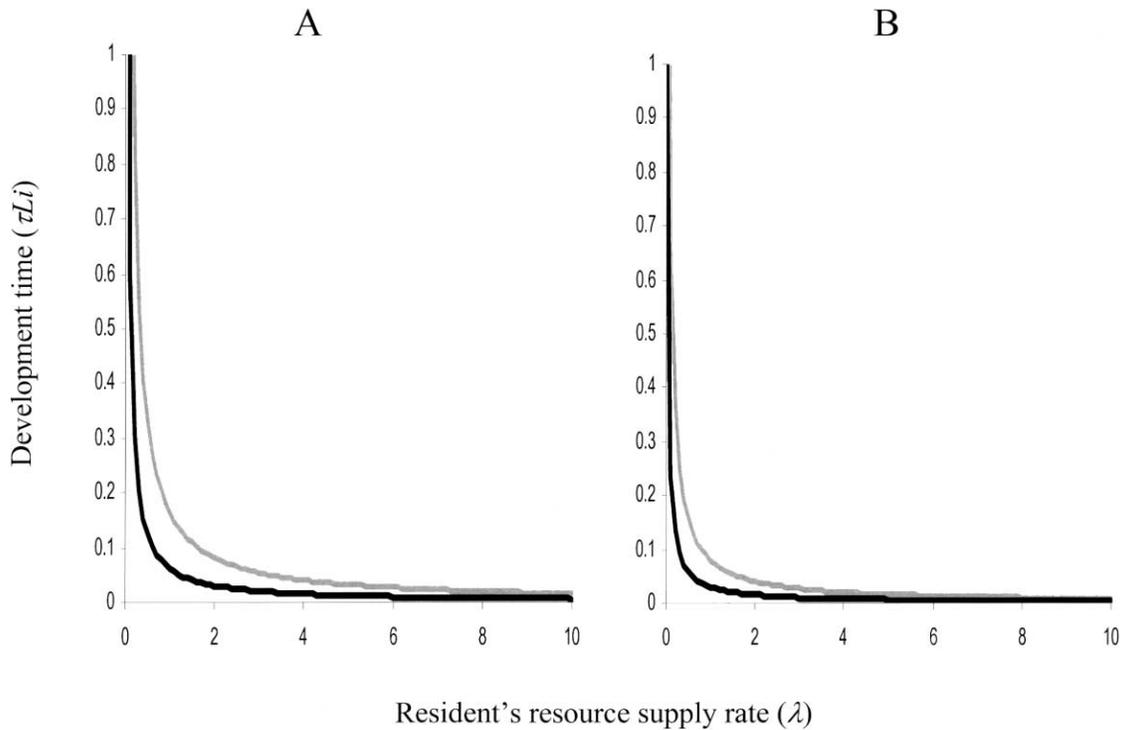
A

B

Figure 3: Invasion boundaries (*gray line*) with respect to the resident strategy (*black line*) for the invasion of a second consumer into an established resource/consumer/natural enemy interaction under a Type II feeding response by vulnerable consumers and a Type I predation risk. Invasion occurs for parameter values below the gray line. *A*, Invader has a growth rate advantage ($r_{A2} = 6.0$, $d_{L2} = 0.0$). *B*, Invader suffers increased density-independent mortality ($r_{A2} = 6.0$, $d_{L2} = 0.75$). Other parameters: $r_{A1} = 3.0$, $\mu = 0.0$, $\beta_1 = \beta_2 = 0.1$, $a_1 = a_2 = 0.1$, $b_1 = b_2 = 0.0001$, $d_{A1} = d_{A2} = 1.0$, $d_{L1} = 0.0$, $d_P = 1.0$, $\tau E1 = \tau E2 = 1.0$, $\sigma_{E1} = \sigma_{E2} = 1.0$, $\tau JP = 1.0$, and $\sigma_{JP1} = \sigma_{JP2} = 1.0$.

sible because of the labile response of the exposed development stage. Now one may observe long-term (though not permanent) coexistence of nearly equivalent species. This is feasible because differences in life-history characteristics (host growth rate, natural enemy attack rate) are outweighed by the interaction between the resource and the consumer's development time. Equivalence in demographic parameters is appropriate for evaluating the potential for long-term transient coexistence under shared enemy interactions.

In figure 3, the solid black lines denote the changes in resident development time ($\tau L1$) as the resource supply rate (λ) increases. At low resource supply, development times are long, while at high resource supply, development times are short. The invasion boundary (when an invader has a higher growth rate than the resident and is expected to win out in apparent competition) is denoted by the gray line (fig. 3*A*). Invasion by a second consumer is, in comparison to the resident, determined by its development time ($\tau L2$) and the resident's resource supply (λ). Here, coexistence becomes possible under high resource supply

as the two consumer species converge on equivalent demographic characteristics ($\tau L1 \approx \tau L2$). Strong and rapid exclusion due to apparent competition is then only prevalent at intermediate resource supply rates where differences in the demographic characteristics between the resident and the invader are sufficient to lead to the exclusion of one of the species by the shared natural enemy. Changes in particular life-history parameters may influence this pattern. For example, if the invader suffers increased density-independent mortality ($d_{Lj} \rightarrow 1$), then coexistence (through convergence to equivalence in demographic characteristics) of the invader and the resident at low productivities may be more likely (fig. 3*B*). Notwithstanding, the main conclusions remain unaltered. Apparent competition is prevalent at intermediate levels of productivity while long-term transient coexistence of nearly equivalent species occurs at high resource supply rates.

Invasion by a second consumer under a Type II feeding response and a Type II predator functional response to each consumer also show similar patterns. The functional response is more complex and now accounts for handling

of each of the vulnerable consumer classes (i and j) by the predator. The form of the function is $g(P) = (\beta_i \times P)/(1 + \gamma \times L_i + \gamma \times L_j)$. In the absence of the second resource-consumer interaction (and allowing $\mu \rightarrow 0$), the following equilibria for the resource/consumer/natural enemy interaction can be obtained:

$$R_1^* = \frac{\lambda}{(a \times L_1^* - \lambda \times b)}, \tag{32}$$

$$L_1^* = \frac{d_P}{\beta_1 \times \sigma_{JP1} - d_P \times \gamma}, \tag{33}$$

$$A_1^* = \frac{L_1^* \times [g(P_1^*) + d_{L1}]}{(r_{A1} \times \sigma_E - d_{A1})}, \tag{34}$$

$$P_1^* = \frac{\left[-\ln\left(\dfrac{d_{A1}}{r_{A1} \times \sigma_{E1}}\right) - d_{L1} \times \tau L1^*\right] \times (1 + \gamma \times L_1^*)}{\beta_1 \times \tau L1^*}, \tag{35}$$

$$\tau L1^* = \frac{m_1}{a} \times \left(\frac{1}{R_1^*} + b\right). \tag{36}$$

The invasion criteria for a second consumer invading an established resource/consumer/natural enemy interaction now takes the form

$$\tau L2 < \frac{\ln\left(\dfrac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right)}{\left(\dfrac{\beta_2 \times P_1^*}{1 + \gamma \times L2 + \gamma \times L_1^*} + d_{L2}\right)}. \tag{37}$$

Since the second consumer is rare, $L2 \rightarrow 0$, and the invasion criteria is of the form

$$\tau L2 < \frac{\ln\left(\dfrac{r_{A2} \times \sigma_{E2}}{d_{A2}}\right)}{\left(\dfrac{\beta_2 \times P_1^*}{1 + \gamma \times L_1^*} + d_{L2}\right)}. \tag{38}$$

Here, however, the invasion condition is a more complicated expression accounting for the equilibrium density of P_1^* (and the nonlinear functional response) and the equilibrium density of resident vulnerable consumers (L_1^*). Boundaries of invasion are shown in figure 4. Again, under more complex feeding and functional responses, strong apparent competitive interactions leading to rapid exclusion are predicted to be most prevalent at intermediate levels of productivity. In low or high productivity environments, coexistence is expected. This arises because

differences in life-history characteristics that lead to the effects of apparent competition (host growth rate, natural enemy attack rate) are outweighed by the interaction between the resource and the consumer development time. Differences in demographic processes (such as increased predator longevity, $d_P \rightarrow 0$) act to scale the invasion criteria rather than qualitatively changing the invasion conditions (fig. 4B).

Invasion into Nonequilibrial Assemblages

If the resource/consumer/natural enemy interaction is unstable and exhibits limit cycles, then the invasion criteria are determined by evaluating the long-term temporal mean abundances of predator and prey in the interaction (Levins 1979; Armstrong and McGehee 1980). For instance, when the single resource/consumer/natural enemy interaction undergoes limit cycles, then the long-term per capita growth rate of the populations must be zero. To analyze invasion by the second prey species and conditions for coexistence, we used numerical studies, integrating equations (1)–(7). Under these conditions, invasion is permissible over a wider range of parameter values than observed under equilibrium conditions (fig. 5). Note the differences in scale between figures 4 and 5. The dominant effects of apparent competition and rapid exclusion are observed under low to intermediate productivity environments. At high levels of enrichment, these indirect effects are not strong, because the interaction between each consumer and its resource tends to outweigh the interaction between the consumer and the natural enemy. Time to exclusion is likely to be longer as species converge on demographic equivalence in high productivity environments (fig. 5).

Dynamics

Since there is no closed form for the equilibria of the full three-species interaction, dynamics can only be explored numerically. As expected, the dynamics are heavily influenced by the two single resource/consumer/natural enemy interactions and in particular the donor-controlled mechanism of density dependence (app. A). In low resource productivity environments (with a Type II feeding response and linear predation), stable or damped oscillations to a stable point dynamics are observed (fig. 6A). As enrichment occurs, the single resource/consumer/natural enemy interaction is unstable, leading to likely extinction (app. B). The inclusion of an additional consumer allows the interaction to persist on a limit cycle attractor (fig. 6B). At high levels of nutrient enrichment, persistence of the indirect interaction is still feasible and may induce aperiodic dynamics (fig. 6C, 6D). Notwithstanding, the
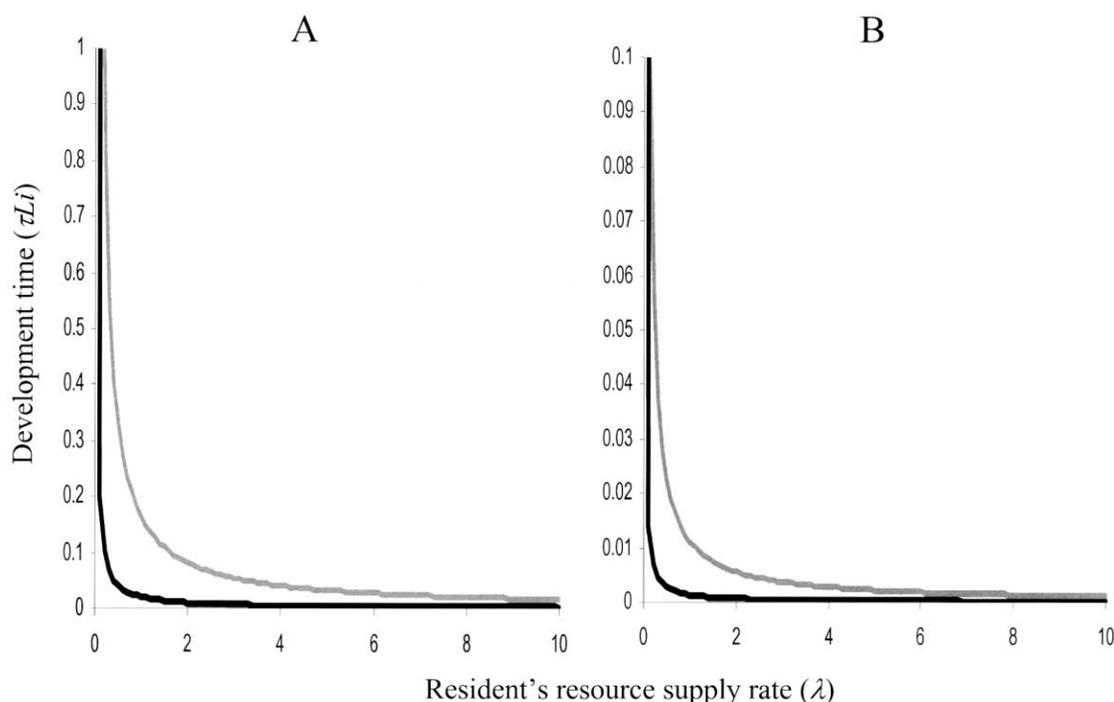
Figure 4: Invasion boundaries (*gray line*) with respect to the resident strategy (*black line*) for the invasion of a second consumer into an established resource/consumer/natural enemy interaction under a Type II feeding response by vulnerable consumers and a Type II predation risk. Invasion occurs for parameter values below the gray line. *A*, Invader has a growth rate advantage ($r_{A2} = 6.0$, $d_P = 1.0$). *B*, The natural enemy is long-lived ($r_{A2} = 6.0$, $d_P = 0.1$). Other parameters: $r_{A1} = 3.0$, $\mu = 0.0$, $\beta_1 = \beta_2 = 0.1$, $\gamma = 0.0001$, $a_1 = a_2 = 0.1$, $b_1 = b_2 = 0.0001$, $d_{A1} = d_{A2} = 1.0$, $d_{L1} = d_{L2} = 0.0$, $\tau E1 = \tau E2 = 1.0$, $\sigma_{E1} = \sigma_{E2} = 1.0$, $\tau JP = 1.0$, and $\sigma_{JP1} = \sigma_{JP2} = 1.0$.

presence of an additional consumer species that feeds on a different resource allows the interaction to persist. This arises through the increase in the number and magnitude of the density dependent processes acting to regulate the interaction.

Enrichment increases natural enemy cycle amplitude but has little effect on the overall amplitude of the consumer populations (results not shown). The effects of enrichment are to decouple the resource-consumer and consumer–natural enemy interactions by increasing consumer density dependence (mediated through the development delay) and decreasing the overall impact of the predator on the two consumer populations.

Discussion

Here we have shown that the level of productivity can determine the outcome of invasion by apparent competitors. In the absence of other limiting factors and effective predators, the interaction between two consumers and their shared natural enemy is not expected to persist at a deterministic equilibrium (Holt 1977; Bonsall and Hassell 1997). In simple models, at high production, resource lim-

itation is weak to nonexistent, so the sole prey species that persists is the one that can withstand the higher levels of attack by the natural enemy or that has the higher population growth rate (Holt and Lawton 1993, 1994). This conclusion emerges from analysis of models in which the criteria for coexistence emerge from deterministic analysis of mutual invasibility. At a broader perspective, competitive equivalents can persist together in long transients even though deterministic coexistence does not occur. Our results suggest that this scenario is more likely to be observed in some environmental conditions than in others. In the scenario we have explored, however, high productivity facilitates the rapid passage of each prey species through the vulnerable phase of its life history. This leads to a more complex relationship between apparent competition and productivity, with the greatest impact of shared predation on rapid exclusion arising at intermediate productivities. Our results also illustrate the potential importance of the detailed dynamics of species' life histories, even when considering broad issues (e.g., indirect interactions) at the community level. Examining the impact of life-history variation is a largely unexplored area of community ecology (but see Chase 1999).
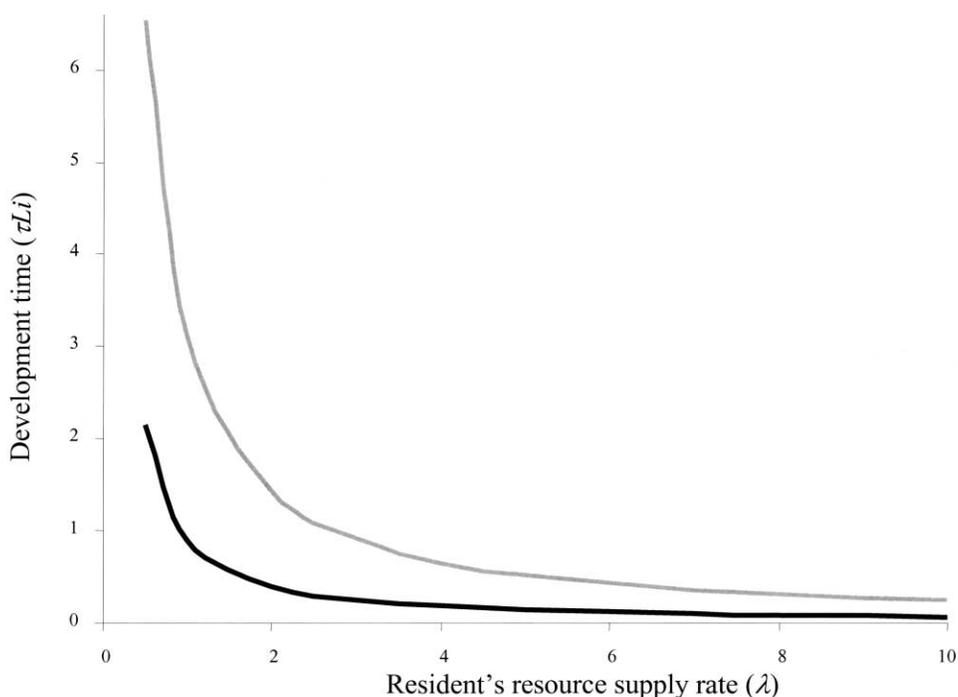
Figure 5: Invasion boundaries for the second consumer (*gray line*) with respect to the resident strategy (*black line*) evaluated under unstable resource/consumer/natural enemy interaction. Invasion occurs for parameter values below the gray line. Cyclic dynamics broaden the conditions under which a second consumer may invade (cf. figs. 4 and 5). Parameters: $r_{A1} = 3.0$, $r_{A2} = 6.0$, $\mu = 0.0$, $\beta_1 = \beta_2 = 0.1$, $a_1 = a_2 = 0.1$, $b_1 = b_2 = 0.0001$, $d_{A1} = d_{A2} = 1.0$, $d_P = 1.0$, $d_{L1} = d_{L2} = 0.0$, $\tau E1 = \tau E2 = 1.0$, $\sigma_{E1} = \sigma_{E2} = 1.0$, $\tau JP = 1.0$, and $\sigma_{JP1} = \sigma_{JP2} = 1.0$.

As in other studies of structured multispecies predator-prey interactions (Briggs 1993; Briggs et al. 1993; Bonsall et al. 2002), a knowledge of the determinants of life-history traits can lead to a number of novel predictions about the dynamics and structuring mechanisms of predator-prey assemblages. In simple models, the interaction between two consumers that share a common natural enemy is not persistent when resources are abundant, and indeed exclusion is more rapid at high levels of productivity. By considering predator-prey interactions with additional biological complexity (while retaining a degree of model tractability), we have illustrated how a subtle (but biologically realistic) regulatory mechanism can influence the persistence and stability of resource/consumer/natural enemy and more reticulate indirect interactions. At low resource levels, few predators should be sustained. At high resource levels, the effects of apparent competition are expected to be mitigated by the positive influence of resources on the rate of consumer development through the vulnerable stage. Only under intermediate levels of productivity are the dynamical effects of this indirect interaction likely to be observed with the rapid exclusion of one of the consumers. This matches a conjecture put forth by one of us (Holt 1997*a*), although the mechanism con-

sidered there (direct predator density dependence combined with saturating functional responses) was quite different from that considered here.

Enrichment

Enrichment of prey populations is well known theoretically to destabilize predator-prey interactions. This "paradox of enrichment" (Rosenzweig 1971) leads to increased amplitude of cycles in pairwise interactions. Several studies have examined whether such systems should persist (May 1973; Yodzis and Innes 1992), while other studies have explored why enrichment may fail to destabilize predator-prey interactions (Gilpin 1972, 1975; Leibold 1989; Abrams and Walters 1996). Two mechanisms postulated to account for the lack of a "paradox of enrichment" are prey refuges and predator density dependence.

Here, the effects of enrichment on the single resource/consumer/natural enemy interaction have been shown to lead to the classic effects of enrichment: destabilization of the predator-prey interaction leading to increasing amplitude cycles. Prey refuges (through the presence of a fixed long-lived invulnerable stage) have little impact on the effects of enrichment. In general, permitting development
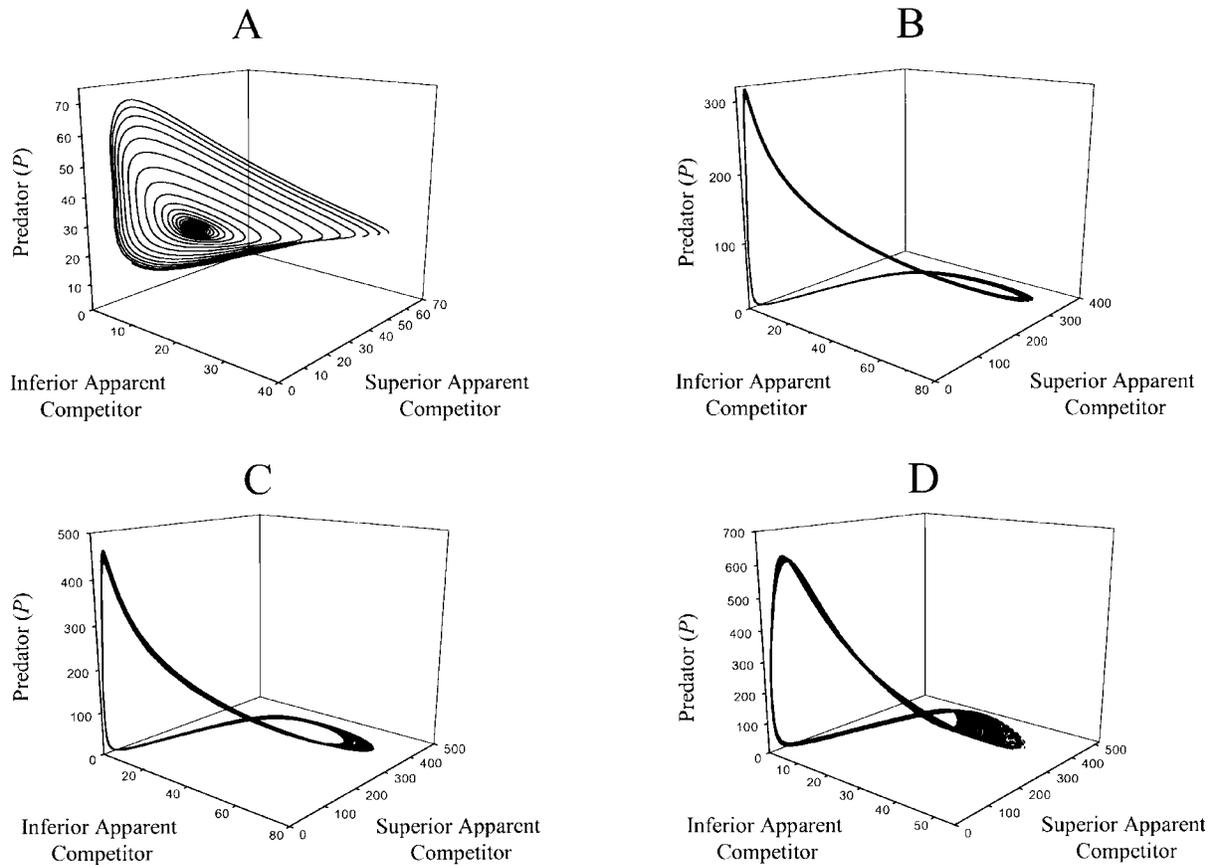
Figure 6: Dynamical attractors for the full three-species interaction (shown in the adult consumer 1, consumer 2, and natural enemy plane) under (*A*) low ($\lambda = 2.0$), (*B*) intermediate ($\lambda = 4.0$), (*C*) high ($\lambda = 6.0$), and (*D*) very high ($\lambda = 10.0$) levels of productivity. Dynamics shift from stable points to limit cycle and then to seemingly aperiodic oscillations within increasing enrichment. In this example, along a gradient in productivity, there is a tendency for predator abundance to increase (on average), but this does not drive consumer 1 to extinction. Other parameters: $r_{A1} = 3.0$, $r_{A2} = 6.0$, $\mu = 0.0$, $\beta_1 = \beta_2 = 0.03$, $a_1 = a_2 = 0.1$, $b_1 = b_2 = 0.001$, $d_{A1} = d_{A2} = 1.0$, $d_P = 1.0$, $d_{L1} = d_{L2} = 0.0$, $\tau E1 = \tau E2 = 1.0$, $\sigma_{E1} = \sigma_{E2} = 1.0$, $\tau JP = 1.0$, and $\sigma_{JP1} = \sigma_{JP2} = 1.0$.

to be labile enhances the region of stable population dynamics (app. B). The system is driven by the interaction between the top-down effects of predation and the bottom-up effects of resource. This latter process acts through a development delay; low predator attacks favor stable dynamics even at relatively high levels of enrichment.

In multispecies predator-prey interactions, such as apparent competition and intraguild predation, the role of enrichment is intrinsically more complicated. Predator functional and numerical responses to alternative prey have the potential to lead to either apparent competition or apparent mutualisms (Abrams et al. 1998). With constraints on the numerical response (through predator density dependence), alternative prey may not interact or may even experience a net gain through the indirect interaction (Abrams and Matsuda 1996), particularly in nonequilibrial situations (Abrams and Walters 1996; Abrams 1999).

Changing productivity has been shown empirically to have equivocal effects on multispecies trophic interactions. Balčiūnas and Lawler (1995) reported that increased nutrient availability in protist-shared enemy interactions increased the likelihood of extinction of predators (not prey) due to the increased abundance of invulnerable individuals. Under intraguild predation, protist consumers and predators may coexist at high levels of productivity (Morin 1999). However, Diehl and Feißel (2000) show that coexistence in similar protist assemblages with intraguild interactions is more likely at intermediate levels of productivity (see also Holt and Polis 1997). It is clear that the detailed interaction structures of food web modules are instrumental in shaping dynamical responses to enrichment (Kaunzinger and Morin 1998).

Although empirical investigations on the role of apparent competition under different productivity regimes

are lacking, enemy-mediated effects are believed to determine the spatial distribution of alternative prey at a variety of different scales (Holt 1984; Schmitt 1987; Holt and Lawton 1994). This scale dependency is known to affect the type of interaction between species sharing natural enemies and can have important consequences for the outcome of apparent competition (Chaneton and Bonsall 2000). Predictions from our study suggest that it is likely that the interaction (e.g., strongly asymmetric vs. equivalency) between the same species pairs will vary over a productivity gradient. This environmental dependency complicates the task of elucidating the role of shared enemies in structuring predator-prey assemblages.

Coexistence

In this study, we have examined how enrichment can affect the dynamics and the coexistence of apparent competitive interactions. Enriching environments is likely to destabilize the interaction and increase cycle amplitudes. This alters prey growth rate, prey density dependence, and predator efficiency and consequently should affect the potential coexistence of consumers that share predators. The presence of an additional resource-consumer interaction can foster the persistence of the pairwise predator-prey interactions even under high levels of productivity (see fig. 6).

Population cycles are expected in single predator-prey interactions with effective predators and weak resource limitation for the prey. Interactions between predator and prey are driven by an implicit time lag in the numerical response of the predator to changes in prey density, leading to repeated episodes of overexploitation, population crashes, and recovery. However, the dynamics of predator-prey interactions are also known to be influenced by the shape of the prey isocline (Rosenzweig and MacArthur 1963; Rosenzweig 1969) and the levels of resource enrichment (Rosenzweig 1971). The factors that govern the persistence of strong trophic interactions along productivity gradients have been widely debated. The consensus emerging from empirical and theoretical studies is that a wide range of biological and ecological factors restrict the domain of application of the paradox of enrichment (Murdoch and McCauley 1985; Leibold 1989; Abrams and Walters 1996). Similarly, in more complex consumer-predator interactions, the coexistence of consumers can be strongly affected by population instabilities and enrichment. Abrams (1999) illustrated how consumers that compete directly for resources and share a predator are less likely to coexist when the dynamics are unstable. Increased productivity increases the temporal variability of consumer population dynamics (Levins 1979) and, coupled with the predator functional and numerical responses, makes the conditions for coexistence even more stringent. This contrasts with the pattern we have observed. The character of the relationship between species richness and productivity is thus expected to be sensitive to the pattern and strength of interactions among species (e.g., the presence or absence of exploitative competition for shared resources). This diversity of responses of species richness to enrichment expected on theoretical grounds may help explain the observed diversity of patterns of richness along productivity gradients (Waide et al. 1999).

Since the average of a nonlinear function is not the function of the averages (Jensen's inequality; see Hardy et al. 1934), higher moments such as the variance of resources or covariances among resource-consumer or consumer-predator interactions and environmental covariates can affect the conditions for coexistence (Levins 1979; Armstrong and McGehee 1980; Abrams 1999). We have observed that coexistence between apparent competitors is at least as likely under limit cycles as it is under stable equilibria. This occurs because the variable time delay introduces a subtle regulatory mechanism into the interaction between resource and consumer. Any factor that reduces the interspecific effects of shared predation or increases the intraspecific processes leading to direct density dependence can promote the persistence of otherwise nonpersistent apparent competitive interactions. Density dependence in prey indirectly reduces the predator's numerical response, thus moderating the potential impact of apparent competition. Coexistence arises due to the nonlinearities (in a multidimensional sense) in the resource/consumer/natural enemy interactions. In particular, fluctuations in the resources driven by the interaction with the consumer modulate the development time, favoring coexistence in unstable and stable systems.

Concordant with earlier studies (e.g., Rosenzweig 1971; Gilpin 1972), our study highlights how simple interactions such as resource/consumer/natural enemy systems can be unstable, leading to diverging oscillations as enrichment occurs. The more reticulate structure of the indirect interaction arising with generalist predators decreases the average interaction strength between the predator and any given prey species (through a reduction in vulnerability to predation) and allows the persistence of the module (McCann et al. 1998). In our model, increasing module complexity, although inherently destabilizing, can also promote persistence. Additional links act to dampen the diverging oscillations and increase the importance of the donor-controlled mechanisms of regulation that promote the persistence of predator-prey assemblages.

Finally, our results bear on current debates about the primary factors organizing community structure (Bell 2000; Hubbell 2001). Our models suggest that along an environmental gradient, apparent competition between alternative prey species may lead to strong exclusion at mod-

erate productivities, but at high productivity the same species may be effectively equivalent, permitting long-term transient coexistence.

The debate over food web structure and dynamics has focused on whether basal resources or top predators structure intermediate trophic assemblages (Hairston et al. 1960; Menge and Sutherland 1976, 1987; Hunter and Price 1992; Leibold 1996). The current consensus is that although predation can affect the dynamics of interactions, resources act concordantly in structuring assemblages. Competition for resources and predation often act simultaneously to influence coexistence or exclusion in multispecies predator-prey interactions through processes such as intraguild predation or apparent competition. Shared enemy interactions are one of the major determinants of the distribution and abundance of interacting species (Holt and Lawton 1994; Bonsall and Hassell 1997). We believe the model discussed here, which pertains to many insect predator-prey systems, elucidates principles under which species involved in apparent competition might coexist in enriched environments. These systems are also capable of a range of dynamical states, including sustained nonequilibrial coexistence. Our results suggest some important phenomena that can arise when structured population models are embedded in community interactions and, in particular, reveal novel ways that top-down and bottom-up effects may be intertwined via a species' basic life history. Such effects warrant much more theoretical and empirical scrutiny.

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