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Impact of Intraguild Predation and Stage Structure on Simple Communities along a Productivity Gradient

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ABSTRACT: We analyze the consequences of intraguild predation and stage structure for the possible composition of a three-species community consisting of resource, consumer, and predator. Intraguild predation, a special case of omnivory, induces two major differences with traditional linear food chain models: the potential for the occurrence of two alternative stable equilibria at intermediate levels of resource productivity and the extinction of the consumer at high productivities. At low productivities, the consumer dominates, while at intermediate productivities, the predator and the consumer can coexist. The qualitative behavior of the model is robust against addition of an invulnerable size class for the consumer population and against addition of an initial, non-predatory stage for the predator population, which means that the addition of stage structure does not change the pattern. Unless the top predator is substantially less efficient on the bottom resource, it tends to drive the intermediate species extinct over a surprisingly large range of productivities, thus making coexistence generally impossible. These theoretical results indicate that the conditions for stable food chains involving intraguild predation cannot involve strong competition for the bottommost resource.

Keywords: competition, food webs, life-history omnivory, model, size refugia, structured populations.

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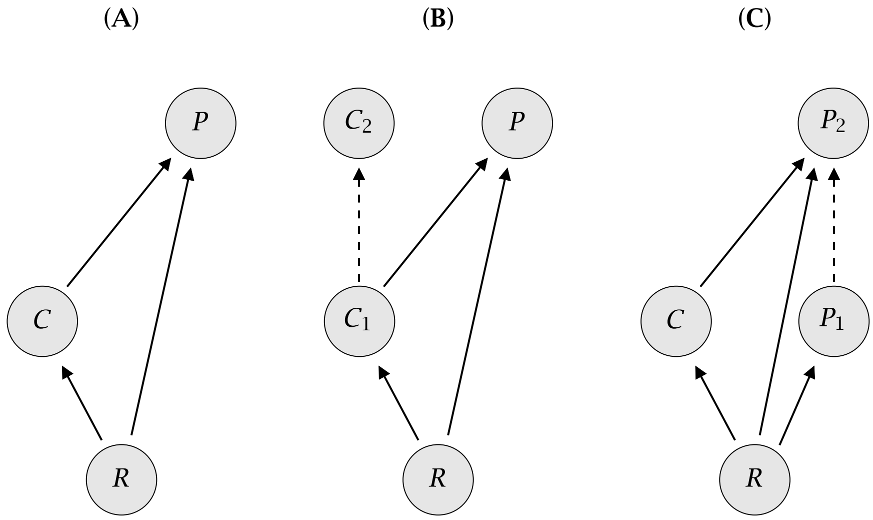

Figure 1: Different cases of IGP and stage structure analyzed in this paper. **A**, Basic intraguild predation. Species P (predator) preys on species C (consumer), and, in addition, P and C compete for a common resource R. **B**, Structured consumer case. As A but with a second consumer stage (C_2) that is invulnerable to predation. **C**, Structured predator case. As A but with an initial stage for the predator (P_1) that feeds exclusively on the resource. Solid arrows reflect feeding interactions, and dashed arrows reflect growth transitions.

Introduction

In food web theory, omnivory is defined as the act of feeding by one species on resources at different trophic levels (Pimm and Lawton 1978). Earlier empirical research led to mixed opinions on whether omnivory is ubiquitous or rare in natural ecosystems (Pimm 1982; Holt and Polis 1997). Additionally, theoretical studies suggested that the occurrence of omnivory destabilizes certain food chains as compared to linear food chain models (Pimm and Lawton 1978; Holt and Polis 1997). This fitted well with the general idea that complex ecosystems tend to be unstable (May 1973) and would imply that omnivory is rare in nature. For these reasons, omnivory has long been a relatively neglected subject of research. However, there are numerous examples of omnivory in natural ecosystems (Pimm and Lawton 1978; Polis and Holt 1992; Diehl 1993, 1995) and the current view is that omnivory is widespread (Winemiller 1990; Polis 1991; Polis and Strong 1996; Persson *et al.* 1996).

One of the simplest conceivable examples of omnivory is a constellation of three species (see graphical representation in fig. 1A): a predator (*top*), a consumer (*middle*) and a resource (*bottom*) that is common to both consumer and predator. This case is also known as “intraguild predation” (IGP; see Polis *et al.* 1989; Holt and Polis 1997). By definition, IGP is a combination of exploitative competition and predation interactions. It is distinguished from competition by the immediate energetic gains for the predator and differs from classical predation because the predation interaction reduces potential exploitative competition (Polis *et al.* 1989; Polis and Holt 1992).

Polis and Holt (1992) suggested that coexistence of a top predator, an intermediate consumer, and a resource in a simple IGP system is possible if the intermediate consumer is superior at exploitative competition for the common resource. Holt and Polis (1997) confirmed this necessary condition by analyzing "community modules" with IGP and added the condition that the top predator should gain significantly from its consumption of the intermediate consumer. Theory also predicts that the productivity level of the resource is important for stability and coexistence (Polis *et al.* 1989). Furthermore, Holt and Polis (1997) hypothesized that there is a potential for alternative stable states if the top predator is relatively inefficient at consuming the intermediate species and that coexistence of predator and consumer is most likely at intermediate levels of resource productivity. These hypotheses were corroborated by Diehl and Feißel (2000) in a combined theoretical and laboratory study on the effects of enrichment on a three-species omnivory system. Diehl and Feißel (2000) provide the most detailed treatment so far, but a comprehensive analysis of IGP in simple food webs and the response to different levels of productivity is still lacking. Recent field experiments on arthropod assemblages (Fagan 1997) and laboratory experiments on protozoan/bacterial microcosms (Holyoak and Sachdev 1998; Morin 1999; Diehl and Feißel 2000) underline the importance of such an analysis.

Intraguild predation is especially likely to occur in systems with stage- or size-structured populations. Individual growth in size often induces ontogenetic diet shifts (see various chapters in Ebenman and Persson 1988). For example, during development, individuals of predatory species with large adult size tend to grow through size ranges that are comparable to their future prey species. Young (small) individuals of the predatory species thus utilize resources that are similar to those used by the prey species. As a result of an increase in individual size of the predatory species, this primary competitive interaction later on shifts to a predator–prey interaction. In many (especially aquatic) systems, different life stages of species tend to feed at different trophic levels. Werner and Gilliam (1984) consider this to be a special case of "ontogenetic niche shifts" and Pimm and Rice (1987) call this phenomenon "life-history omnivory".

These size-related ontogenetic shifts may give rise to conflicting demands on individual morphology and to trade-offs among features that adapt species to alternate ontogenetic niches (see Ebenman and Persson 1988). Consequently, individual traits may be a compromise between selection pressures that operate in different parts of the life cycle. This may subsequently set constraints on how competitive an individual can be at each stage of its life cycle. A species that is a predator as an adult and undergoes substantial shifts in niche during its life cycle is likely to have lower overall competitiveness than a species undergoing less substantial niche shifts. For example, individuals of a prey species may be better competitors for shared resources than juvenile individuals of a predatory species. In this case, they can limit the recruitment of predator individuals to larger size classes, even though resources for these larger size classes may not be limited. This phenomenon is called a "juvenile competitive bottleneck" (Persson 1987; Persson and Greenberg 1990). Juvenile competitive bottlenecks thus represent a mechanism that amplifies the competitive superiority of the consumer relative to the predator. This competitive superiority was postulated by Holt and Polis (1997) as a necessary condition for the coexistence of consumer and predator in community modules with IGP.

The occurrence of stage structure will decrease the interaction strength between the species. Pimm and Rice (1987) studied life-history omnivory in Lotka–Volterra models of aquatic food webs, and concluded that life-history omnivory reduces stability much less than single-life-stage omnivory does. Holt and Polis (1997) suggested that stage structure *per se* may promote coexistence between the intermediate consumer and the top predator. Other recent theoretical developments (McCann and Hastings 1997; McCann *et al.* 1998) indicate that "weak links" connecting a species with others in a food web tend to promote community persistence and stability.

The aim of this study is to investigate the consequences of incorporating intraguild predation and stage structure into a standard model describing a three-link linear food chain (*e.g.*, Oksanen *et al.* 1981; DeAngelis *et al.* 1996). In the first part, we analyze a basic model with IGP by the top species (see fig. 1A). We give a comprehensive analysis of the community structure predicted by this basic IGP model, focusing on the relative competitiveness of the top species and the intermediate species, as a function of the resource productivity. We define the community structure as the species presence and abundance over the collection of population-dynamical attractors of the system, depending on the values of the parameters. We concentrate on two types of questions. First, how large is the region in parameter space where coexistence of predator, consumer, and resource is possible, and, especially, how relevant is the "intermediate level of productivity" where coexistence could occur (Holt and Polis 1997; Diehl and Feißel 2000)? Second, in what parameter region does the possibility of alternative stable states (Holt and Polis 1997) occur, and what does this tell us about the relevance of these phenomena for natural ecosystems? After the basic model, we analyze the effects of stage structure to test the hypothesis that it promotes coexistence between top predator and intermediate consumer as suggested by Holt and Polis (1997). To do this, we extend the basic IGP model to include a size refuge for the consumer, by introducing a second consumer class which is invulnerable to predation (fig. 1B), and stage structure in the predator population, with an initial predator stage that feeds only on the resource and a second stage that feeds on the consumer as well as on the resource (fig. 1C).

The Basic IGP Model

Model Formulation

We considered the following basic IGP model, describing the dynamics of a top species or predator (P), an intermediate species or consumer (C), and a bottom species or resource (R):

$$\frac{dP}{dt} = \frac{e_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + e_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C}\, P - \mu_{\mathrm{p}}\, P\,, \tag{1}$$

$$\frac{dC}{dt} = \frac{e_{\mathrm{rc}}\, a_{\mathrm{rc}}\, R}{1 + h_{\mathrm{rc}}\, a_{\mathrm{rc}}\, R}\, C - \frac{a_{\mathrm{cp}}\, C}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C}\, P - \mu_{\mathrm{c}}\, C\,, \tag{2}$$

$$\frac{dR}{dt} = \rho\,(K - R) - \frac{a_{\mathrm{rc}}\, R}{1 + h_{\mathrm{rc}}\, a_{\mathrm{rc}}\, R}\, C - \frac{a_{\mathrm{rp}}\, R}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C}\, P\,. \tag{3}$$

According to this model (depicted schematically in fig. 1A), the consumer population feeds on the resource only, whereas the predator population feeds on the resource as well as on the consumer. Both predator and consumer populations decline by natural mortality, and the consumer experiences an additional mortality due to predation. We assume that in the absence of consumers and predators the resource population grows according to semichemostat dynamics. Parameter ρ represents the inflow rate, and K represents the equilibrium density of the resource in the absence of consumers and predators (*i.e.*, a measure of the productivity).

All feeding interactions follow a Holling Type II functional response (*i.e.*, consumption rates become saturated as food densities increase). The parameters h_{cp}, h_{rp}, and h_{rc} represent the handling times corresponding to the consumer being eaten by the predator, the resource being eaten by the predator, and the resource being eaten by the consumer, respectively. The predator feeds on the consumer with attack rate a_{cp}. The attack rates on the resource by the consumer and by the predator (a_{rc} and a_{rp}, respectively) express the competitive superiority of the consumer over the predator: a_{rc} is larger than a_{rp}. The energy derived by consumption of resource is channeled into consumer and predator offspring with conversion efficiencies e_{rp} (for the predator) and e_{rc} (for the consumer). Analogously, consumer individuals are converted into predator offspring with efficiency e_{cp}. Hence, both functional and numerical responses are nonlinear. Parameters μ_p and μ_c denote the mortality rates of both populations. A summary of the variables and parameters is given in table 1.

Parameterization

We parameterized the model for the interaction between Eurasian perch (*Perca fluviatilis*) as top species or predator, roach (*Rutilus rutilus*) as intermediate species or consumer, and zooplankton (*e.g.*, *Bosmina* or *Daphnia*) as bottom species or resource. Perch, roach, and zooplankton represent a typical IGP system with stage structure. Juvenile small perch compete with roach for zooplankton, whereas adult perch potentially become piscivorous and prey upon roach (Persson 1988; Persson and Greenberg 1990).

The values of attack rates, handling times, and conversion efficiencies for resource consumption were calculated for perch individuals with a body mass of 184 g, roach with a body mass of 3.0 g, and a small-bodied zooplankton resource consisting of 0.5-mm *Bosmina*. All rates were scaled to a daily basis.

Numerical values for the attack rate on the resource by the consumer (a_{rc}), the handling time (h_{rc}), and the conversion efficiency (e_{rc}) were estimated using the formulas presented in Persson *et al.* (1998). Roach and young perch are roughly similar with respect to these parameters, so we assumed handling times and conversion efficiencies concerning the zooplankton resource to be equal for the consumer and the predator. The consumer handling time of the predator has been calculated using data from Christensen (1997). For the calculation of the conversion efficiencies e_{rp} and e_{cp} (converting resource and consumer individuals, respectively, into predator offspring) we assume that both prey types of the predator have the same weight per unit of volume and equal digestive and energetic properties. Hence, consumer conversion efficiency e_{cp} differs only from the resource conversion efficiency e_{rp} by a multiplication factor representing the weight ratio of consumer to resource individuals. We assume that

Table 1: Definitions of model variables and parameters, and their default numerical values.

Symbol	Value	Unit	Description
		Predator	
P	...	$\mathrm{ind_p \cdot L^{-1}}$	Population density
a_{cp}	$1 \cdot 10^{+2}$	$\mathrm{L \cdot d^{-1} \cdot ind_p^{-1}}$	Consumer attack rate
h_{cp}	0.11	$\mathrm{d \cdot ind_p \cdot ind_c^{-1}}$	Consumer handling time
e_{cp}	0.3	$\mathrm{ind_p \cdot ind_c^{-1}}$	Consumer conversion efficiency
a_{rp}	$5 \cdot 10^{+2}$	$\mathrm{L \cdot d^{-1} \cdot ind_p^{-1}}$	Resource attack rate
h_{rp}	$5 \cdot 10^{-5}$	$\mathrm{d \cdot ind_p \cdot ind_r^{-1}}$	Resource handling time
e_{rp}	$1 \cdot 10^{-5}$	$\mathrm{ind_p \cdot ind_r^{-1}}$	Resource conversion efficiency
μ_{p}	0.05	$\mathrm{d^{-1}}$	Natural mortality rate
m_{p}	Varied	$\mathrm{d^{-1}}$	Maturation rate [a]
		Consumer	
C	...	$\mathrm{ind_c \cdot L^{-1}}$	Population density
a_{rc}	$5 \cdot 10^{+3}$	$\mathrm{L \cdot d^{-1} \cdot ind_c^{-1}}$	Resource attack rate
h_{rc}	$5 \cdot 10^{-5}$	$\mathrm{d \cdot ind_c \cdot ind_r^{-1}}$	Resource handling time
e_{rc}	$1 \cdot 10^{-5}$	$\mathrm{ind_c \cdot ind_r^{-1}}$	Resource conversion efficiency
μ_{c}	0.05	$\mathrm{d^{-1}}$	Natural mortality rate
m_{c}	Varied	$\mathrm{d^{-1}}$	Maturation rate [b]
		Resource	
R	...	$\mathrm{ind_r \cdot L^{-1}}$	Population density
ρ	0.5	$\mathrm{d^{-1}}$	Semichemostatic inflow rate
K	Varied	$\mathrm{ind_r \cdot L^{-1}}$	Stand-alone equilibrium density

Note: All volume units are in liters (L), and all time units are in days (d).

[a] Only in structured predator model.

[b] Only in structured consumer model.

consumer and predator suffer from the same natural mortality. All standard parameter values are given in table 1.

By varying the value of K, we investigated the effect of different productivities on the existence and stability of the various types of population-dynamic attractors. Furthermore, we varied the attack rates of the predator on both the consumer and the resource in order to evaluate the consequences of different predation pressures and competition strengths.

Equilibria

The steady states of the model are derived by setting the right-hand sides of equations (1)–(3) to 0, and solving the resulting system of equations for the unknown population densities. There are four possible equilibria: the "resource equilibrium", in which only the resource is present; the "consumer equilibrium", in which both the consumer and the resource are present; the "predator equilibrium", in which the predator and the resource are present; and the "consumer–predator equilibrium", in which all species are present.

In the resource equilibrium, both the consumer and the predator are absent, and hence, the resource is present at its equilibrium density K. In the consumer equilibrium, only the predator is absent ($P = 0$). The equilibrium densities of the resource, $\hat{R}_c$, and consumer, $\hat{C}_c$, can be found by first substituting $P = 0$ in equation (2), setting its right-hand side to 0, and solving for R. Substituting $\hat{R}_c$ obtained in this way, together with $P = 0$, in equation (3) yields the following expressions for the equilibrium densities of the resource and consumer populations:

$$\hat{R}_c = \frac{\mu_c}{a_{rc}\,(e_{rc} - h_{rc}\,\mu_c)}\,, \qquad \hat{C}_c = \frac{\rho\, e_{rc}}{\mu_c}\left(K - \frac{\mu_c}{a_{rc}\,(e_{rc} - h_{rc}\,\mu_c)}\right). \tag{4}$$

In the predator equilibrium, only the consumer is absent. The densities of resource and predator in this equilibrium, $\hat{R}_p$ and $\hat{P}_p$, respectively, can be derived in the same way as above, by substituting $C = 0$ in equation (1), solving for R, and substituting $\hat{R}_p$ and $C = 0$ in equation (3):

$$\hat{R}_p = \frac{\mu_p}{a_{rp}\,(e_{rp} - h_{rp}\,\mu_p)}\,, \qquad \hat{P}_p = \frac{\rho\, e_{rp}}{\mu_p}\left(K - \frac{\mu_p}{a_{rp}\,(e_{rp} - h_{rp}\,\mu_p)}\right). \tag{5}$$

In the consumer–predator equilibrium, all species are present. From equation (1), a linear relationship between the equilibrium values $\hat{R}_{cp}$ and $\hat{C}_{cp}$ can be derived. By substituting this expression in equations (2) and (3), one variable (C) can be eliminated, resulting in a system of two equations with two unknowns (P and R). In appendix A, we show that up to two plausible solutions exist. Only one of these solutions defines a stable equilibrium with resource, consumer, and predator.

Effect of Varying the Productivity Level

In this section, we study the existence and stability of the four equilibria mentioned above as well as their dependence on the productivity level of the resource. We used a mixture of analytical and numerical techniques; the latter was performed with the help of CONTENT (Kuznetsov *et al.* 1996), an interactive

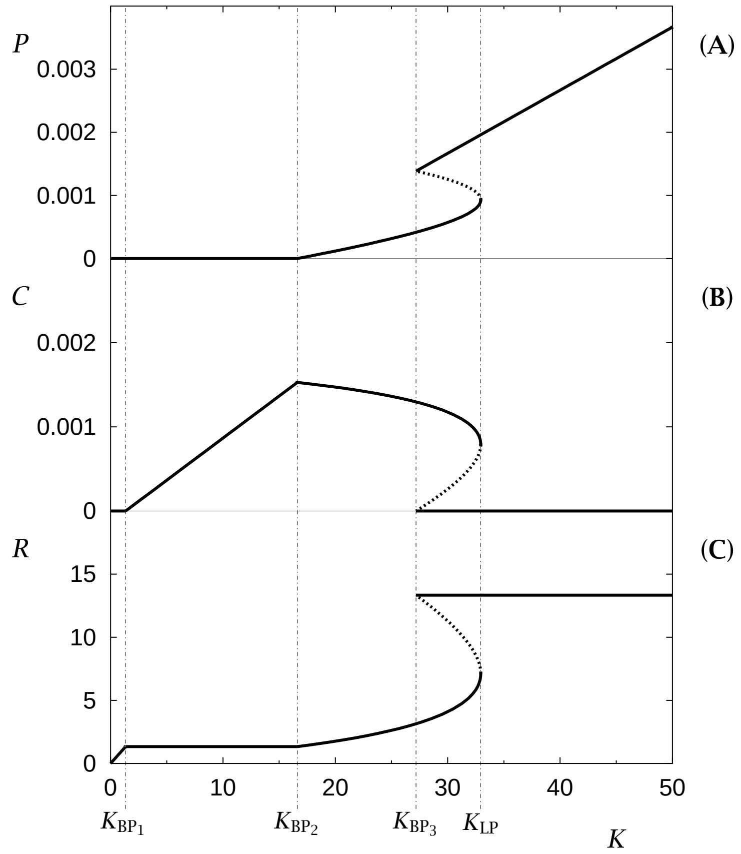

Figure 2: Steady states of the basic IGP model (1)–(3) along a productivity gradient. **A**, Equilibrium values of the predator population density. **B**, Equilibrium values of the consumer population. **C**, Equilibrium values of the resource. Solid curves denote stable equilibria, dotted curves unstable ones. Parameter values are listed in table 1.

software package for numerical bifurcation analysis of dynamical systems (see Kuznetsov 1998 for an introduction and overview).

Using CONTENT, we determined the spectrum of qualitative behavior of our models depending on the values of the parameters, most notably the productivity level and the attack rates. We detected and located all equilibria, checked for other bifurcation points, and continued all bifurcation points while varying the parameter values. The software enabled us to determine the stability of equilibria based on monitoring their eigenvalues. Analytical checks and simulation experiments corroborated the numerical analysis. No singular points other than stable and unstable equilibria were present.

In figure 2, the equilibria of the basic IGP model (1)–(3) are plotted against productivity, which is parameterized as the equilibrium density of the resource population if the higher trophic levels are absent, K. We will compare this pattern with the basic pattern for a three-link resource–consumer–predator food chain as described by Oksanen *et al.* (1981).

At very low productivities, neither the consumer nor the predator population can maintain itself, and only the resource level increases with increasing productivity. In the absence of the predator, the differential equation for the consumer [eq. (2)] can be reduced to

$$\frac{dC}{dt} = \frac{e_{rc}\, a_{rc}\, R}{1 + h_{rc}\, a_{rc}\, R}\, C - \mu_c\, C\,. \tag{6}$$

Dividing the right-hand side by C yields the growth rate of the consumer population in the absence of the predator. The consumer can enter the system in resource equilibrium if this rate is positive:

$$\frac{e_{rc}\, a_{rc}\, R}{1 + h_{rc}\, a_{rc}\, R} > \mu_c\,. \tag{7}$$

In the resource equilibrium, the resource is present at density K. Consequently, substitution of $R = K$ in equation (7) yields the condition for successful invasion of the consumer into the resource equilibrium:

$$K > \frac{\mu_c}{a_{rc}\,(e_{rc} - h_{rc}\,\mu_c)}\,. \tag{8}$$

We define the productivity level given by the right-hand side of equation (8) as K_{BP_1}. (The subscript "BP" stands for "branching point", because at this point a new equilibrium curve branches off in the bifurcation diagram.) For the parameter values given in table 1, $K_{BP_1} = 1.33\ \mathrm{ind_r \cdot L^{-1}}$ (see fig. 2).

At K values beyond K_{BP_1}, the equilibrium density of the consumer increases linearly with the productivity, whereas the resource stays at a constant level. At these productivities, and for the default parameter values in table 1, the consumer excludes the predator because the latter requires foraging on the former to offset its competitive inferiority on the resource. However, in this region, consumer densities are too low to compensate. The predator can invade the consumer equilibrium if its growth rate (when present at low densities) exceeds 0:

$$\frac{e_{rp}\, a_{rp}\, R + e_{cp}\, a_{cp}\, C}{1 + h_{rp}\, a_{rp}\, R + h_{cp}\, a_{cp}\, C} > \mu_p\,. \tag{9}$$

With increasing productivity and correspondingly increasing consumer densities, this inequality will eventually become satisfied, which enables the predator to invade the system. The productivity level at which this happens we call K_{BP_2} (see fig. 2). At productivities larger than K_{BP_2}, a stable steady state exists with positive population densities of both consumer and predator. For completeness, we mention that K_{BP_2} is almost equal to the K value where the consumer–predator equilibrium would start off in the model without IGP (*i.e.*, the three-link linear food chain; *cf.* Oksanen *et al.* 1981). The additional resource is hardly advantageous for the predator, as the resource density set by the consumer is far below the half-saturation value for the predator's functional response.

From this point, differences start to arise with the basic pattern for a three-link linear food chain as described by Oksanen *et al.* (1981). Without IGP, the predation strength of the predator and the density of its prey determine the minimum productivity level at which the predator will be able to invade the system. Furthermore, beyond the invasion point of the predator, the intermediate consumer density remains at a constant level, whereas both the resource and predator population densities increase with productivity. In the case of intraguild predation, the predator is able to persist at lower productivities due to the exploitation of an additional food resource, and the consumer density declines with increasing productivity due to competition with the predator.

In addition, the predator can persist on the resource alone in the absence of the consumer provided the resource level is sufficiently high. Substituting $C = 0$ and $R = K$ in equation (9) yields the following invasion criterion:

$$K > \frac{\mu_{\mathrm{p}}}{a_{\mathrm{rp}}\,(e_{\mathrm{rp}} - h_{\mathrm{rp}}\,\mu_{\mathrm{p}})} \,. \tag{10}$$

In figure 2, this inequality is satisfied at $K > 13.3$ $\mathrm{ind_r \cdot L^{-1}}$ (slightly below K_{BP_2}). However, the predator equilibrium will be unstable as long as it can be invaded by the consumer. The corresponding invasion criterion, which is derived in appendix B, is neutral at K_{BP_3} (see fig. 2). For K values higher than K_{BP_3}, the consumer cannot invade, which results in a stable predator equilibrium, where the predator can maintain itself on the resource exclusively.

Beyond the productivity level K_{LP}, the consumer–predator equilibrium vanishes. (The subscript "LP" stands for "limit point", because this point is the upper limit of the values of parameter K for which the equilibrium exists.) Consequently, the basic IGP model shows bistability for K between K_{BP_3} and K_{LP}. In this interval, two alternative stable equilibria are present: the predator equilibrium and the consumer–predator equilibrium. Which equilibrium will be attained (*i.e.*, whether the predator will eliminate the consumer or not) depends on the initial population densities.

At productivities higher than K_{LP}, the high densities of the basic resource enable the predator to eliminate the consumer, regardless of the initial conditions. In this case, the predator can persist solely on the resource, and the predator equilibrium is the only stable steady state remaining.

Effect of Varying the Attack Rates

So far, we have identified four critical productivity levels at which a change occurs in the number and/or stability of the possible equilibria (fig. 2: K_{BP_1}, K_{BP_2}, K_{BP_3}, and K_{LP}). The numerical values of these bifurcation points will, of course, depend on the foraging capacities of both the consumer and the predator on the resource as well as on the predation intensity of the predator on the consumer. The possible configurations of the different stable states of the system can best be understood by varying the attack rates of the predator on the resource (a_{rp}) and on the consumer (a_{cp}). Notice that parameter a_{rp} is inversely proportional to $\hat{R}_{\mathrm{p}}$ [eq. (5)], the competitive ability of the predator on the resource *sensu* Tilman (1982), and, likewise, a_{cp} characterizes the predation ability of the top species. Bifurcation analyses (using CONTENT; see Kuznetsov *et al.* 1996) reveal that other parameters (handling times, conversion efficiencies, and mortality rates; see table 1) either have only quantitative effects or their effects can easily be expressed in terms of the attack rates using equations (4), (5), and (8)–(10).

Figure 3 shows combinations of a_{rp} (on the abscissa) and a_{cp} (on the ordinate) that limit the regions of existence of the consumer, the predator and the consumer–predator equilibria. The curve labeled C_{LP} indicates those combinations of parameters a_{rp} and a_{cp} at which the productivity threshold $K_{\mathrm{LP}} = 32.94$ $\mathrm{ind_r \cdot L^{-1}}$. [The latter is the value of K_{LP} in fig. 2, for ease of comparison. Notice that the point $(a_{\mathrm{rp}}, a_{\mathrm{cp}}) = (500, 100)$ on curve C_{LP} in fig. 3 corresponds with the limit point at $K = 32.94$ in fig. 2.] Curve C_{LP} limits the region of

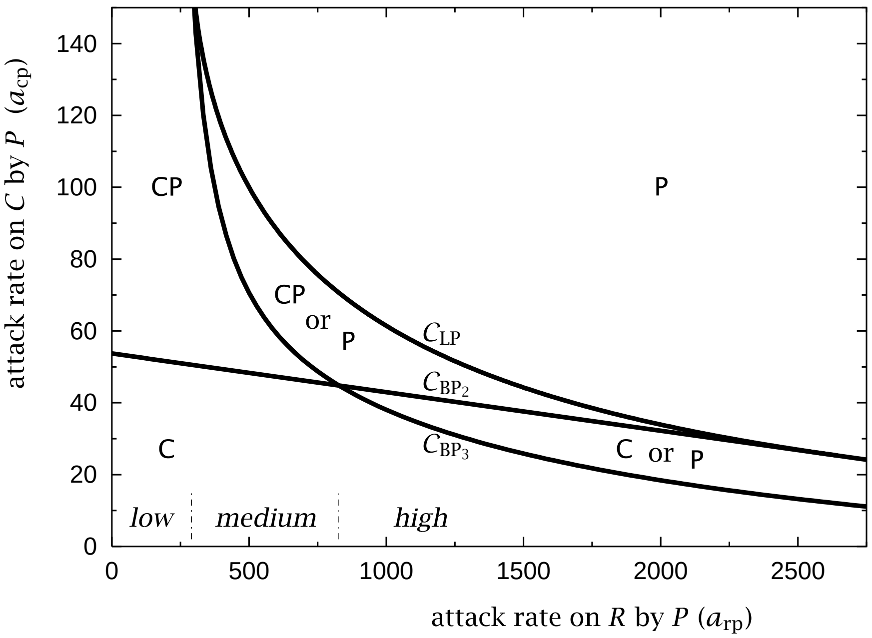

Figure 3: Effect of the attack rates a_{rp} and a_{cp} on the existence of possible equilibria of the basic IGP model (1)–(3). Curve C_{LP} corresponds to K_{LP}, curve C_{BP_2} to K_{BP_2}, and curve C_{BP_3} to K_{BP_3} (*cf.* fig. 2). For every region bounded by these curves, the stable steady states are indicated: P denotes the predator equilibrium, C the consumer equilibrium, and CP the consumer–predator equilibrium. The variable $K = 32.94\ \mathrm{ind_r{\cdot}L^{-1}}$, and the other parameters have values as listed in table 1.

existence of the consumer in the system (for the parameter values listed in table 1; see also fig. 2). Above this curve, the predator eliminates the consumer, regardless of the initial conditions.

Curve C_{BP_2} analogously indicates the combinations of a_{rp} and a_{cp} at which the second productivity threshold (K_{BP_2}) is equal to K. Along this curve, the invasion criterion for the predator into the consumer equilibrium (see fig. 2) is neutral. The area above the curve reflects the values of a_{rp} and a_{cp} for which the predator can invade the consumer equilibrium. Below curve C_{BP_2}, the predator is not able to enter a system in which the consumer is present.

Curve C_{BP_3} indicates the combinations of a_{rp} and a_{cp} at which $K_{\mathrm{BP}_3} = K$. This curve represents neutrality of the invasion criterion for the consumer into the predator equilibrium. Below the curve, the consumer can always invade the predator equilibrium. For $(a_{\mathrm{rp}}, a_{\mathrm{cp}})$ combinations situated above curve C_{BP_3}, the consumer is not able to enter a system in which the predator is already present.

The mathematical expressions for curves C_{BP_2} and C_{BP_3} are given in appendix B. We also derived an analytical expression for curve C_{LP} but as it is too complicated to be easily interpretable, we have not listed it.

The three curves in figure 3 divide the $(a_{\mathrm{rp}}, a_{\mathrm{cp}})$ parameter space into five different regions. For the parameter combinations in the regions C, P, and CP, respectively, the consumer equilibrium, the predator equilibrium, and the consumer–predator equilibrium are the only stable steady states present. In region C (*i.e.*, for low values of both a_{rp} and a_{cp}), the top species is neither a good competitor nor a good predator and, hence, cannot become established. For the parameter combinations in region P, the top species is a relatively strong competitor as well as an efficient predator (a_{rp} and a_{cp} are high) and thereby is able to eliminate the consumer from the system. In region CP (*i.e.*, for low values of a_{rp}), the top species is a bad exploiter of the resource but a relatively good predator. In this area, the system closely resembles a three-link food chain.

The transitions in figure 3 can be explained biologically as follows: For "low" values of the predator's resource consumption rate (a_{rp}), the predator is a poor competitor for the common resource and totally depends on the consumer as a food source. As long as the predation rate on the consumer (a_{cp}) is also low, the top species will be excluded. Consequently, the only stable steady state of the system is the consumer equilibrium (area C). However, if the predation rate on the consumer is high, then the top species can invade the consumer equilibrium, which results in a stable three-link food chain of resource, consumer and predator (area CP). Notice that only at these low values of a_{rp}, where IGP is effectively absent, can the predator not exclude the consumer from the system.

Starting at a point where the predator just cannot enter the consumer equilibrium (below curve C_{BP_2}), increasing its ability to feed on the resource can temporarily promote coexistence between consumer and predator (*i.e.*, moving horizontally to the right, crossing curve C_{BP_2} in fig. 3). However, the region in parameter space where this can happen is small ($\approx 34 < a_{\mathrm{cp}} < 53$ for the default parameter set) as compared to the size of the total parameter interval with coexistence (areas CP and 'CP or P'). The coexistence interval (for a_{cp}, K, or other parameters) is also strictly decreasing with a_{rp}. Moreover, for a_{cp} smaller than ≈ 40, the curve C_{LP} will almost immediately be crossed as well, and then the consumer–predator equilibrium vanishes.

At "intermediate" values of the predator's resource consumption rate, different patterns emerge as the predation rate is increased. At low predation rates, the consumer equilibrium is still the only stable steady state (area C), and as soon as the predator is able to invade the consumer equilibrium (crossing of curve C_{BP_2}), a stable consumer–predator equilibrium results (area CP). When the predation rate is further increased, the invasion boundary for the consumer (curve C_{BP_3}) is also crossed, and the predator equilibrium becomes stable (area 'CP or P'). The consumer cannot invade this boundary P equilibrium because of predation pressure, even though the interior CP equilibrium with both consumers and predators still exists and is stable. This bistability can be explained because in this area the intermediate species exploits the resource far more efficiently than the top species. The top species can survive on merely the resource, but if the consumer is already established in the system, it will lower the density of the resource to such an extent that the top species becomes dependent on the intermediate species as an additional food source. This results in an alternative stable steady state with both species present. If the predation rate increases even more, curve C_{LP} is crossed, and the predator equilibrium is the only stable equilibrium remaining (area P). In this area, predation is not only high enough to prevent invasion by the consumer but, when combined with exploitation of the additional resource, is also sufficient to eliminate the consumer population.

At “high” resource attack rates for the predator, the predator equilibrium comes into play before the consumer–predator equilibrium. With increasing predation rate, curve C_{BP_3} is crossed first, and the predator equilibrium arises (area 'C or P'). The predator cannot invade a system in which the consumer is present because of the low density of the resource population. The consumer, however, cannot escape predation long enough to invade the predator equilibrium. Hence, both single-species equilibria are stable, and initial densities determine which one will be attained. If the predation rate on the consumer exceeds the levels bounded by curve C_{BP_2}, predation is again high enough for the predator to invade any system, whether the consumer is present or not (area 'CP or P'). At still higher predation pressures, the predator unconditionally excludes the consumer from the system (area P).

To conclude, the basic IGP model predicts exclusion of the predator at low productivities and exclusion of the consumer at high productivities. Coexistence of consumer and predator —potentially accompanied by the occurrence of alternative stable states— is only possible in a relatively small range of intermediate productivity levels (see fig. 2). This extends and complements Diehl and Feißel's (2000) conclusions, which were reached in the context of a very general IGP model analysis, but under the assumption that population dynamics converged to equilibrium states, and illustrated by numerical examples of a Lotka–Volterra-type model with logistic resource growth and linear functional responses. They were also able to draw conclusions on abundance patterns based on assumptions about the signs of the interaction terms, whereas we could provide a complete bifurcation pattern of the IGP system.

Likewise, when analyzing the effect of different resource and consumer attack rates of the predator, we see (fig. 3) that coexistence and alternative stable states are relatively rare. When the predator is an inefficient resource feeder (*i.e.*, approximately back in the linear food chain situation), increasing its predation efficiency leads (from a consumer–only state) to coexistence between consumer and predator. For a relatively small resource consumption efficiency (as compared to the consumer), increasing the predation efficiency will eventually replace the consumer–predator coexistence by a predator monopoly. Before the predator's resource consumption efficiency is of the same order of magnitude as that of the consumer, the coexistence window has disappeared completely. In that situation, varying the predation efficiency shows a switch between the consumer and the predator equilibria, with a relatively small region of overlap.

Adding IGP to a linear food chain (*left* in fig. 3) will generally decrease the possibility of consumer–predator coexistence. Only if starting in a consumer-only situation when the predator can almost invade, will increasing its ability to feed on the resource promote coexistence. However, as we have seen, the parameter region for which this can happen is relatively small. In addition, from an ecological perspective, increasing the intraguild predator's resource-feeding ability will decrease its ability to prey on the consumer because the predator faces a trade-off between its predator and consumer capabilities. Even when this trade-off is very weak (*i.e.*, a_{cp} decreases only slightly with a_{rp}), the system will tend not to cross curve C_{BP_2}, where the predator can invade the consumer equilibrium. Instead of moving horizontally across figure 3, the system will move more downward. In this case, regions CP or 'CP or P' will generally not be entered because the invasion criterion for the predator in the consumer equilibrium is hardly dependent on a_{rp}.

The limited possibility for coexistence of consumer and predator, and especially the poor performance of the consumer, raises the question of whether or not we have oversimplified intraguild predation. In the introduction, we argued already that IGP and size- or stage-structured populations often go hand in hand. Therefore, in the following sections, we will add structure to the consumer and the predator populations in the basic IGP model.

The IGP Model with a Structured Consumer Population

In this section, we see whether structure in the consumer population, by means of the introduction of an invulnerable consumer life stage, can counter the observed predator dominance at high productivities. In other words, we assume a size refuge for larger individuals: only small consumer individuals are susceptible to predation. Invulnerable stages leading to partial escape have been suggested to promote coexistence between predators and consumers (Hambright 1994; Holt and Polis 1997). This may help the consumer to withstand predation and persist at high productivities.

Model Formulation

We extend the basic model (1)–(3) in the following way (*cf.* fig. 1B):

$$\frac{dP}{dt} = \frac{e_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + e_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C_1}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C_1}\, P - \mu_{\mathrm{p}}\, P\ , \tag{11}$$

$$\frac{dC_2}{dt} = m_{\mathrm{c}}\, C_1 - \mu_{\mathrm{c}}\, C_2\ , \tag{12}$$

$$\frac{dC_1}{dt} = \frac{e_{\mathrm{rc}}\, a_{\mathrm{rc}}\, R}{1 + h_{\mathrm{rc}}\, a_{\mathrm{rc}}\, R}\,(C_1 + C_2) - \frac{a_{\mathrm{cp}}\, C_1}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C_1}\, P - (m_{\mathrm{c}} + \mu_{\mathrm{c}})\, C_1\ , \tag{13}$$

$$\frac{dR}{dt} = \rho\,(K - R) - \frac{a_{\mathrm{rc}}\, R}{1 + h_{\mathrm{rc}}\, a_{\mathrm{rc}}\, R}\,(C_1 + C_2) - \frac{a_{\mathrm{rp}}\, R}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C_1}\, P\ . \tag{14}$$

The consumer population is now divided into two classes: a class consisting of small individuals vulnerable to predation (with density C_1) and an invulnerable class containing larger individuals (C_2). Notice that we assume that both classes exploit the resource at the same rate and that they convert all energy derived from resource consumption into small, vulnerable consumer offspring. An alternative would be to assume that the vulnerable individuals do not reproduce, which would favor the predator. The presented model variant thus represents a best-case scenario for the persistence of the consumer population.

The density of the invulnerable consumer class decreases only by natural mortality and increases due to maturation. The vulnerable consumer population declines not only because of natural mortality and predation (as in the basic model) but, in this case, also because of maturation into large invulnerable consumers with rate m_{c}.

All parameter values are identical to those used in the basic model (see table 1). If the newly introduced maturation rate $m_{\mathrm{c}} = 0$ then the extended model is identical to the basic model. We evaluated the consequences of increasing the maturation rate for the possible equilibrium states of the model.

Results

Quantitatively, the introduction of an invulnerable-consumer life stage hinders predator invasion at low K values and promotes the elimination of the consumer at higher K values. This helps the consumer to persist at a broader range of productivities. With increasing maturation rate m_{c}, the productivity thresholds K_{BP_2}, K_{BP_3}, and K_{LP} shift to higher values, whereas K_{BP_1} stays constant. An example is given in figure 4. Notice that for $m_{\mathrm{c}} = 0$, all thresholds are at the values of the basic model (*cf.* fig. 2).

With increasing maturation rates, a larger part of the consumer population is invulnerable. This causes the shift of the threshold K_{BP_2} (beyond which the predator can invade the consumer equilibrium) to higher K values. If consumer and predator coexist, the average predation pressure on the consumer population is lower, which leads to a slower increase in predator density with productivity. As a consequence, the predator population has to reach higher

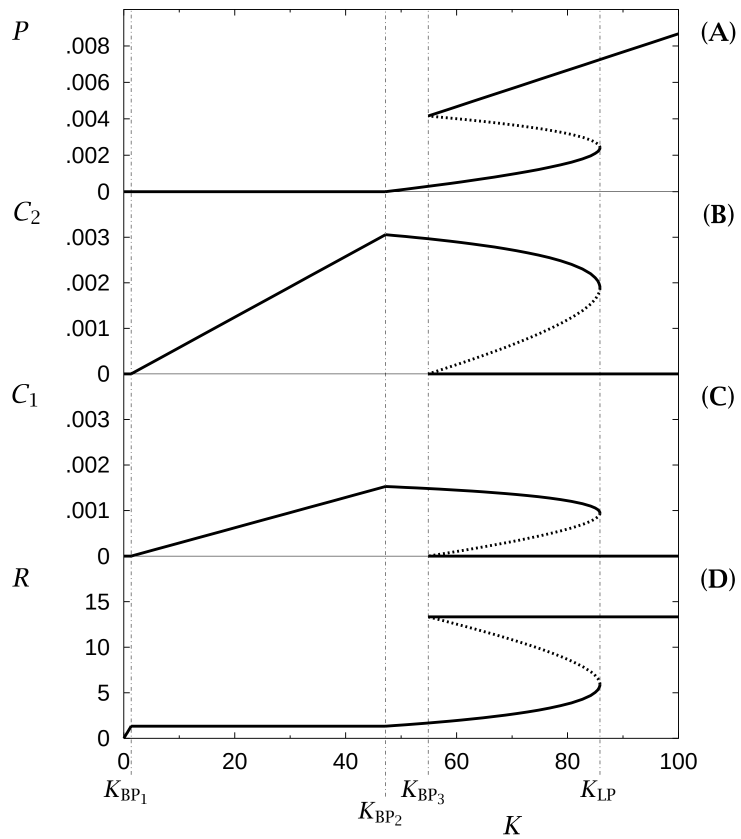

Figure 4: Steady states of the structured consumer model (11)–(14) along a productivity gradient. **A**, Equilibrium values of the predator population density. **B**, Equilibrium values of the invulnerable consumer population. **C**, Equilibrium values of the vulnerable consumer. **D**, Equilibrium values of the resource. *Solid curves*, stable equilibria; *dotted curves*, unstable equilibria. See table 1 for parameter values; $m_c = 0.1\ d^{-1}$.

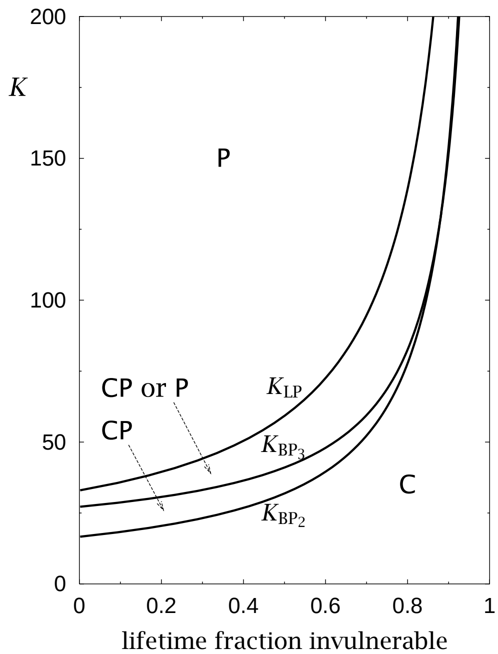

Figure 5: Effect of the relative duration of the invulnerable stage in the structured consumer model on the possible equilibria attained along a productivity gradient. The relative duration, plotted on the abscissa, is given by $\mu_c/(\mu_c+m_c)$. For explanation, see the text. See table 1 for parameter values.

densities to be able to eliminate the consumer from the system. Therefore, threshold K_{LP} is not only shifted to higher productivity values but also occurs at higher population densities. Furthermore, the consumer is able to invade the predator equilibrium at higher productivity values, which can be seen by the shift of threshold K_{BP_3} to higher K values.

Compared with the basic model, the consumer–predator equilibrium occurs over a broader range of K values: the difference between K_{BP_2} and K_{LP} increases with m_c. The region of coexistence, however, shrinks relative to the increasing values of the bifurcation points themselves [$(K_{LP} - K_{BP_2})/K_{LP}$ changes from ≈ 0.5 for $m_c = 0$ (see fig. 2) asymptotically to 0.43 for large m_c]. The value of $(K_{LP} - K_{BP_3})/K_{LP}$ increases from ≈ 0.17 for $m_c = 0$ (fig. 2) asymptotically to 0.49. This means that for large maturation rates, the predator equilibrium can occur at smaller productivities than the consumer–predator equilibrium does and that bistability between the predator equilibrium and the consumer equilibrium is also possible.

When, however, the maturation rate is constant and not too high, the introduction of an invulnerable-consumer class leads to the same qualitative relations between the equilibria and productivity as the basic IGP model. At low productivities, the consumer monopolizes the resource, followed by a stable consumer–predator equilibrium (including a large region of bistability) at intermediate productivities, and a predator monopoly at high productivities.

In figure 5, we show the effect of the magnitude of the maturation rate, parameterized as the relative duration of the invulnerable, initial life stage in the stage-structured population, on the equilibria that can be attained along a productivity gradient. (Notice that this “relative duration” is an *a priori* expectation for a newborn individual, and only due to background mortality and the maturation probability: predation mortality is not taken into account here.)

We varied the expected fraction of the lifetime that an individual consumer spends in the invulnerable class by changing the maturation rate m_c and plotted the values of the bifurcation points K_{BP_2}, K_{BP_3}, and K_{LP}. For reference, notice that the basic IGP model is obtained back when this fraction is 0 (*i.e.*, $m_c = 0$) and that the pattern depicted in figure 4 is located at an invulnerable lifetime fraction of 0.67 in figure 5. The value of K_{BP_1} does not depend on m_c and is, for these parameter values, equal to 1.33 $\mathrm{ind_r} \cdot \mathrm{L}^{-1}$.

From this figure, we see that an increase in the contribution of the invulnerable stage in the structured consumer population (*i.e.*, an increase of m_c) first has little effect on the qualitative model behavior: the main effect is that the values of the branching points and the limit point move up and the K interval for which bistability occurs grows. This is because the consumer takes advantage of its growing size refuge and can invade the predator equilibrium more easily. The K interval for which the consumer–predator equilibrium is the only stable state shrinks with an increasing contribution of the invulnerable stage. The overall picture remains the same. Only if the average consumer individual is expected to spend almost its whole lifetime in the invulnerable stage does the bistable interval completely overlap the consumer–predator coexistence and even some fraction of the interval of the consumer equilibrium. At the same time, however, K_{BP_2} and K_{BP_3}, which represent the lower limits of the existence of the consumer–predator coexistence and the predator monopoly, respectively, move up to extremely high levels of production.

Somatic growth of consumer individuals can be highly dependent on the amount of available resources. An increase in resource availability is likely to result in higher individual growth rates and thereby enhance the rate at which consumer individuals enter the size refuge. We investigated whether such a resource-dependent maturation rate might help the stage-structured consumer to overcome the predator dominance at high productivities by assuming a linear relation between the maturation rate (m_c) and resource availability (R):

$$m_c = \alpha R , \tag{15}$$

with $\alpha > 0$. Substituting this expression in equations (12) and (13) leads to qualitatively identical results (not shown) when compared with a constant maturation rate. As soon as the consumer can persist (at productivity levels beyond K_{BP_1}), it depresses the resource to a constant level, which results in a constant value for m_c. As the predator can invade the consumer equilibrium at productivity levels above K_{BP_2}, the resource density slowly increases with K, resulting in increasing maturation rates. With increasing maturation rates, the productivity thresholds K_{BP_2}, K_{BP_3}, and K_{LP} shift more strongly to higher K values. However, the predator still monopolizes the resource at high productivity.

Thus, to conclude, the invulnerable life stage enables the consumer to persist at higher productivities. The upper limit of the productivity range where consumer–predator coexistence is possible grows, but it also shows a stronger overlap (*i.e.*, bistability) with the productivity range for the predator equilibrium. This means that the domain of attraction of the consumer–predator equilibrium shrinks and that disturbances could cause the system to attain the predator equilibrium instead. These effects become stronger if the lifetime contribution of the invulnerable stage grows, but for dominating invulnerable stages, the consumer–predator coexistence and the predator monopoly no longer occur at realistic levels of production.

The IGP Model with a Structured Predator Population

In this section, we focus on the question of whether an initial life stage for the predator that feeds only on the resource can counter the predator dominance at high productivities. In the life histories of many predator species, ontogenetic shifts separate earlier life stages (with feeding at lower trophic levels) from later life stages (where individuals also feed on the resource).

Model Formulation

We extend the basic model (1)–(3) by adding an initial, nonpredatory class to the predator population (*cf.* fig. 1C):

$$\frac{dP_2}{dt} = m_{\mathrm{p}} P_1 - \mu_{\mathrm{p}} P_2 \,, \tag{16}$$

$$\frac{dP_1}{dt} = \frac{e_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + e_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C} P_2 - (m_{\mathrm{p}} + \mu_{\mathrm{p}}) P_1 \,, \tag{17}$$

$$\frac{dC}{dt} = \frac{e_{\mathrm{rc}}\, a_{\mathrm{rc}}\, R}{1 + h_{\mathrm{rc}}\, a_{\mathrm{rc}}\, R} C - \frac{a_{\mathrm{cp}}\, C}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C} P_2 - \mu_{\mathrm{c}} C \,, \tag{18}$$

$$\frac{dR}{dt} = \rho\,(K - R) - \frac{a_{\mathrm{rc}}\, R}{1 + h_{\mathrm{rc}}\, a_{\mathrm{rc}}\, R} C - \frac{a_{\mathrm{rp}}\, R}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R} P_1 - \frac{a_{\mathrm{rp}}\, R}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, R + h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C} P_2 \,. \tag{19}$$

The predator population is now divided into two subpopulations: an initial class consisting of small individuals (with density P_1) that do not prey on the consumer population and a second, predatory class containing larger individuals (P_2). Both classes exploit the resource at the same rate. Notice that we assume no reproduction taking place by the small individuals in the initial stage. The model we study here thus represents a best-case scenario for enabling the consumer population to also persist at higher productivities.

The density of the second predator stage decreases only by natural mortality and increases due to maturation. The initial-stage predator population declines by means of natural mortality, as in the basic model, and also because of maturation into large individuals, with rate m_{p}.

All parameter values are identical to those used in the basic model and the structured consumer model (see table 1). The structured predator model is asymptotically identical to the basic model when the maturation rate goes to infinity.

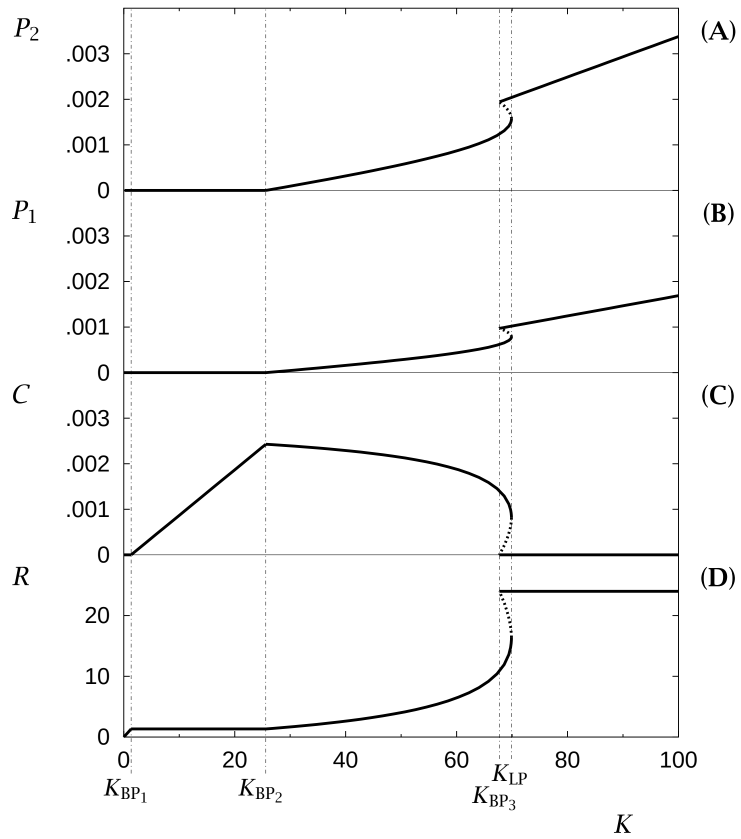

Figure 6: Steady states of the structured predator model (16)–(19) along a productivity gradient. **A**, Equilibrium values of the second-stage predator population density. **B**, Equilibrium values of the initial-stage predator population. **C**, Equilibrium values of the consumer. **D**, Equilibrium values of the resource. *Solid curves*, stable equilibria; *dotted curves*, unstable equilibria. See table 1 for parameter values; $m_{\mathrm{p}} = 0.1\ \mathrm{d}^{-1}$.

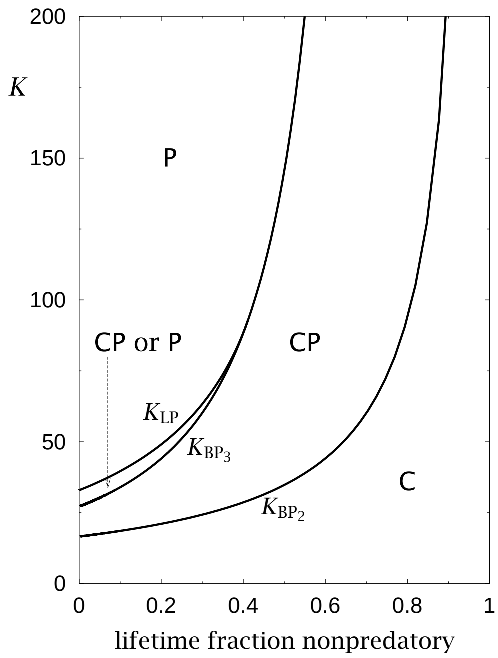

Figure 7: Effect of the relative duration of the nonpredatory stage in the structured predator model on the possible equilibria attained along a productivity gradient. The relative duration, plotted on the abscissa, is given by $\mu_{\mathrm{p}}/(\mu_{\mathrm{p}} + m_{\mathrm{p}})$. For explanation, see the text. See table 1 for parameter values.

Results

In figure 6, we show an example of the steady state values of the structured predator model along a productivity gradient for the case of a constant maturation rate. In this situation, for $m_{\mathrm{p}} = 0.1\ \mathrm{d}^{-1}$, the value of the branching point K_{BP_3} (where the consumer can just invade the predator equilibrium) is almost equal to the value of the limit point of the consumer–predator equilibrium. Consequently, there is only a small productivity interval with bistability. For slightly smaller values of m_{p} (*i.e.*, longer duration of the initial life stage), the predator equilibrium will directly take over from the consumer–predator equilibrium when the productivity increases, and *vice versa*. For higher values of the maturation rate (*i.e.*, shorter initial stage), the situation is qualitatively identical to the basic model.

In figure 7, we show the effect of the relative duration of the nonpredatory life stage. The basic unstructured model is again at the left side of the panel at a nonpredatory fraction of zero ($m_{\mathrm{p}} \to \infty$) and the pattern depicted in figure 6 is located at a nonpredatory fraction of 0.33. Increasing the proportion of time spent in the nonpredatory stage (by decreasing m_{p}) reduces the bistability window; K_{BP_3} moves up faster than K_{LP} because the consumer has less difficulty invading the predator equilibrium. Beyond this, where predator individuals are expected to spend the smaller fraction of their lifetime in the predatory, omnivorous stage, the system behavior is reminiscent of that of a three-link linear food chain: with an increasing level of production, the consumer equilibrium is replaced by a consumer–predator coexistence. If the nonpredatory stage is a dominant element in the predator's life history, then the predator will not be able to maintain itself because of the consumer's superiority in resource competition.

An alternative structured predator model would result if we were to assume that the resource consumption stage and the predatory stage disjunctively correspond to the initial and the second life stage, respectively. Effectively, this would bring the system back to the linear food chain pattern: The top species would not be able to eliminate the intermediate one because, without the intermediate species, second-stage predators have no food available and cannot reproduce.

We also investigated some model variants with a non-constant maturation rate for the structured predator case. A resource-dependent maturation rate, say $m_{\mathrm{p}} = \beta K$ with $\beta > 0$, shows a smaller productivity window for the consumer–predator equilibrium, if the latter exists at all. This is because, in the consumer–predator equilibrium, resource density slowly increases with productivity, which enables the initial-stage predators to mature earlier in life and increases the predation pressure on the consumer population. Differences are buffered because the resource level does not vary with productivity at the consumer and the predator equilibria. For the same reason, alternative scenarios such as an intake-dependent maturation rate yield results similar to the basic structured predator model.

Thus, to conclude, a nonpredatory initial life stage for the predator enables the consumer to persist at higher productivities. The range of productivities where consumer–predator coexistence is possible grows considerably, and bistability disappears when the lifetime contribution of the nonpredatory stage grows. If the nonpredatory stage lasts for more than about half of the expected lifetime, the system is reminiscent of a linear food chain, but the predator monopoly no longer occurs for realistically low levels of production any more. If the nonpredatory stage really dominates the predator's life history, the consumer–predator coexistence also occurs only at very high productivities.

Conclusions and Discussion

There are two major differences between the intraguild predation models analyzed in this article and the corresponding traditional linear food chain models. With IGP, the system exhibits a limited potential for species coexistence due to elimination of the consumer and shows a potential for the occurrence of alternative stable equilibria.

The elimination of the consumer, especially at high levels of resource productivity, is the most conspicuous difference. IGP enables the predator to exist on the resource exclusively and to eliminate the consumer in highly productive systems. This elimination is due to predation and not to resource depletion. As a result, coexistence of resource, consumer, and predator can occur only in a limited parameter region of the IGP models: for intermediate levels of productivity, and a rather precise combination between the predator's attack rates on the resource and on the consumer (*i.e.*, if one of these two rates is large, the other one should be small).

Three situations can be distinguished with respect to the degree of omnivory by the top species. The first one is the case when the predator is a far less efficient resource feeder than the consumer. This condition is rather trivial because this case is closest to the standard three-link food chain to which the omnivorous systems are related: with increasing resource productivity, the stable states of the system are subsequently a resource-only equilibrium, an equilibrium with resource and consumer, and, at high production levels, an equilibrium in which all three levels are present (*cf.* Oksanen *et al.* 1981). The second situation occurs when the resource consumption efficiency of the predator is higher than in the first situation but still significantly lower than that of the consumer. This yields a system in which coexistence of consumer and predator is rare. Moreover, the stability regions of the consumer equilibrium and/or the consumer–predator equilibrium tend to overlap with the stability region of the predator equilibrium. In these regions of bistability, if the system is in the consumer–predator equilibrium, then perturbations can take it away from the basin of attraction of the consumer–predator equilibrium, with convergence to the predator equilibrium as a result. This possibility even further decreases the likelihood for coexistence between consumer and predator. The third situation occurs when the resource consumption efficiency of the predator is of the same order of magnitude as that of the consumer or higher, which leaves no space for coexistence between consumer and predator. This case resembles a one-resource–two-consumer model with competitive exclusion, on the understanding that the top species is, relatively speaking, at an advantage because of its feeding on the intermediate species.

It is worthwhile to recall that only stable and unstable equilibrium states are present along the productivity gradient in our model. This is partly due to the semichemostat resource dynamics and introduces a difference with three-species food chain models where the resource dynamics is modeled by the logistic equation (*e.g.*, Hastings and Powell 1991; McCann and Hastings 1997; De Feo and Rinaldi 1998; McCann *et al.* 1998). These models can show complex behavior (paradox of enrichment cycles, chaos, and multiple attractors) at higher productivities. The semichemostat resource dynamics are an alternative for the logistic dynamics, most notably when the resource has a physical refuge and/or when the resource population includes invulnerably small, albeit mature, size classes that grow into vulnerable size classes. An example is zooplankton on which planktivorous fish feed (Persson *et al.* 1998). The prevalence of equilibrium states instead of complex dynamics enables us to concentrate on the intrinsic effects of the interactions between the species rather than the effects caused by complex resource dynamics that percolate upward in the food web. In this way, we can compare our model predictions with those from equilibrium theories of food chain dynamics (Oksanen *et al.* 1981; DeAngelis *et al.* 1996; Diehl and Feißel 2000). Despite the fascinating results on food webs with complex dynamics (see Abrams and Roth 1994*b*; McCann and Hastings 1997; De Feo and Rinaldi 1998; McCann *et al.* 1998), equilibrium theories still remain a frame of reference in our understanding of food web interactions. That might be even more the case if we consider recent contributions that show that the magnitude of oscillations is bounded by weak amounts of omnivory and allochthonous inputs (McCann and Hastings 1997; Huxel and McCann 1998).

When analyzing the effect of different consumer attack rates of the predator, we see that coexistence and alternative stable states stay relatively rare. When the predator is an inefficient resource feeder (*i.e.*, when the system is approximately in the linear food chain situation), increasing its predation efficiency leads (from a consumer–only state) to coexistence between consumer and predator. For a relatively small resource consumption efficiency (as compared to the consumer), increasing the predation efficiency will eventually replace the consumer–predator coexistence by a predator monopoly. Before the predator's resource consumption efficiency is of the same order of magnitude as that of the consumer, the coexistence window has disappeared completely. In that situation, varying the predation efficiency shows a switch between the consumer and the predator equilibrium, with a relatively small region of overlap.

Overall, we find that the resource feeding efficiency of the predator should be significant but low as compared to the consumer's efficiency in order to make coexistence of predator and consumer possible. In this situation, the basic IGP model and its structured variants all predict competitive exclusion of the predator at low productivities and removal of the consumer at high productivities. This pattern is different from the linear food chain situation (Oksanen *et al.* 1981), where coexistence is the norm at high productivities. In the case of destabilization of the dynamics over an enrichment gradient —related to logistic resource growth— the population abundance of the top species can even decrease, with extinction as a possible result (Abrams and Roth 1994*a*; see also Abrams and Roth 1994*b*). Holt and Polis (1997) stated two criteria for coexistence between predator and consumer to occur. First, the intermediate species should be "superior at exploitative competition for the shared resource" and second, "the top species should gain significantly from its consumption of the intermediate species". The first criterion is substantiated by our analysis, but the second one is too weak. If the predation efficiency is increased, the limit point of the consumer–predator equilibrium will soon be passed.

With respect to alternative states, Holt and Polis (1997) hypothesized that, for systems with intraguild predation, there is a potential for alternative stable states if the top predator is relatively inefficient at consuming the intermediate species. In our basic, unstructured model, bistability only arises at intermediate productivities. For these intermediate K values, the system always exhibits the consumer–predator equilibrium and the predator equilibrium as two alternative stable states. A second possibility of bistability arises when the competitive asymmetry between the predator and the consumer is decreased, for example, if the predator is only a slightly inferior competitor compared with the consumer or if the life history of the predator is characterized by a dominant nonpredatory initial life stage. In such cases, a range of production levels exists where the predator as well as the consumer equilibria will be locally stable.

The introduction of stage structure in the life history of either the intermediate species or the top species (both are likely to occur in omnivorous systems) changes the patterns predicted by the basic model only to a limited extent. An invulnerable stage for the consumer has little effect. Only when we assumed a superlinear increase of the maturation rate of the initial-stage consumer with *productivity* was the stable predator equilibrium replaced by consumer dominance at high productivities. Several reservations can be offered about this assumption. First, it is rather extreme and not substantiated by any biologically valid argument. Second, the biological interpretation of the dependence of maturation rate on productivity level puts the model out of the scope of the framework considered here. In fact, this is an implicit way of modeling an alternative resource (see below) which increases in abundance with environmental productivity.

The introduction of a nonpredatory initial life stage in the omnivorous predator's life history has a larger impact than the introduction of a size refuge in the consumer (*cf.* Figures 5, 7). Only if the initial stage dominates the life history of the predator, does the pattern with productivity change (to a situation reminiscent of that of the linear food chain). This condition would require a very high age at maturity or low mortality rates in the initial life stage. A situation which will also substantially change the patterns is when the second life stage of the predator does not feed on the resource. In this case, the linear food chain pattern is obtained immediately because the predator cannot reproduce and therefore cannot maintain itself without the consumer.

Invulnerable stages, or absolute size refuges in consumer life histories, have been suggested as an explanation for the decoupling of the trophic cascade in food chains. For example, Brönmark and Weisner (1996) stated that in aquatic systems, size refuges may decouple trophic interactions from piscivores to primary producers because primary carnivores (*i.e.*, planktivores and benthivores) reach a size refuge and thereby exert a predation pressure on herbivores despite the presence of piscivores. Likewise, Hambright (1994) suggested that invulnerable stages in a consumer population could prevent predator control. At the top species level, Holt and Polis (1997) hypothesized that a possible mechanism for coexistence between predator and consumer is age-restricted predation, or ontogenetic niche shifts. Our model predicts that coexistence may happen only under special circumstances.

Invulnerable stages for consumers have also been suggested to promote the occurrence of alternative stable states (Paine *et al.* 1985; Bazely and Jefferies 1986). Chase (1999*a*,*b*) shows that in a three-level food chain with consumer size refugia, and a trade-off between early growth to invulnerable size and reproduction at small size, bistability occurs at intermediate productivity. The results from the invulnerable consumer model are in line with these findings. However, at higher degrees of invulnerability and realistic levels of production, these alternative stable states do not occur.

We have seen that models of very different classes yield the same general result, namely, that omnivory increases the probability of intermediate consumer exclusion (*e.g.*, Pimm and Lawton 1977, 1978; Diehl and Feißel 2000, and our results). The building block models analyzed in this paper suggest that Pimm and Lawton (1978) were basically correct concerning the rarity of omnivory under the restricted assumption of simple food chains. At the same time, omnivory seems to be common in natural ecosystems. One can raise the question of whether this discrepancy can be due to the existence of a second (or more) basic resource or resources. Simple calculations suffice to show that the resource density at the productivity level where the consumer can just invade the predator equilibrium (K_{BP_3}) almost maximizes the functional response of the consumer. Hence, the addition of any alternative resource will hardly increase its ingestion. A fundamental observation in this respect is that the consumer exclusion is due to the predation pressure of the top species and not to apparent competition for the resource (*cf.* Diehl and Feißel 2000).

Weakening the link (see also McCann and Hastings 1997; McCann *et al.* 1998) between consumer and predator by introducing an invulnerable stage for the consumer increases the possibility of a consumer equilibrium but decreases the possibility of consumer–predator coexistence. Weakening this link by introducing a nonpredatory stage for the predator does indeed increase the possibility of consumer–predator coexistence, but in this case, omnivory is a negligible factor in the system. Other mechanisms, like physical refuges, differential resource edibility (Leibold 1989), flexible behavior, and habitat complexity (Diehl 1988, 1992), would take us out of the realm of the simple ecosystems considered here but can be expected to have similar effects. In this respect, Briggs (1993; see also Briggs *et al.* 1993) has shown that two competing, stage-structured parasitoid species which attack the eggs and larvae, respectively, of the same host species can coexist under a substantial range of conditions only if the larval parasitoid can also attack larvae already infected by the egg parasitoid. In this particular example, the omnivorous feeding relation increases coexistence of the species. An even better candidate would be a weak link between resource and predator, for example, because the predator only feeds on the resource in a restricted part of its life history. Notice that this assumption would bring the system closer to a linear food chain.

To conclude, our results suggest two plausible explanations for the discrepancy between data and theory concerning the prevalence of omnivory: even though species are capable of omnivorous feeding, their capacity in this respect, and thus the influence on population dynamics, is limited, or mechanisms that protect the intermediate consumer against predation compensate for the influences that would otherwise lead to its extinction. The latter explanation would again imply that omnivory is dynamically negligible. At this stage, our conclusion is that more clarity is needed about what factors enable coexistence of species in simple food webs with omnivory.

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Appendix A The Consumer–Predator Equilibrium

Setting the right-hand side of eq. (1) to 0 and eliminating P yields the following equation in $\hat{R}_{\mathrm{cp}}$ and $\hat{C}_{\mathrm{cp}}$:

$$\hat{C}_{\mathrm{cp}} = \frac{\mu_{\mathrm{p}} - (e_{\mathrm{rp}} - h_{\mathrm{rp}}\,\mu_{\mathrm{p}})\,a_{\mathrm{rp}}\,\hat{R}_{\mathrm{cp}}}{(e_{\mathrm{cp}} - h_{\mathrm{cp}}\,\mu_{\mathrm{p}})\,a_{\mathrm{cp}}}\,. \tag{A1}$$

Besides that, setting the right-hand sides of equations (2) and (3) to 0 and subsequently dividing (2) by C yields two expressions for $\hat{P}_{\rm cp}$:

$$\hat{P}_{\rm cp} = \frac{e_{\rm rc}\, a_{\rm rc}\, \hat{R}_{\rm cp} - \mu_{\rm c}\,(1 + h_{\rm rc}\, a_{\rm rc}\, \hat{R}_{\rm cp})}{a_{\rm cp}} \cdot \mathcal{F}\,, \tag{A2}$$

$$\hat{P}_{\rm cp} = \frac{\rho\,(K - \hat{R}_{\rm cp})\,(1 + h_{\rm rc}\, a_{\rm rc}\, \hat{R}_{\rm cp}) - a_{\rm rc}\, \hat{R}_{\rm cp}\, \hat{C}_{\rm cp}}{a_{\rm rp}\, \hat{R}_{\rm cp}} \cdot \mathcal{F}\,, \tag{A3}$$

with a common factor, $\mathcal{F} := (1 + h_{\rm rp}\, a_{\rm rp}\, \hat{R}_{\rm cp} + h_{\rm cp}\, a_{\rm cp}\, \hat{C}_{\rm cp})\ /\ (1 + h_{\rm rc}\, a_{\rm rc}\, \hat{R}_{\rm cp})$.

Equating the right-hand sides of equations (A2) and (A3) while neglecting the common factor $\mathcal{F}$ (which yields a negative solution) and using equation (A1) gives us

$$\frac{\mu_{\rm p} - (e_{\rm rp} - h_{\rm rp}\, \mu_{\rm p})\, a_{\rm rp}\, \hat{R}_{\rm cp}}{e_{\rm cp} - h_{\rm cp}\, \mu_{\rm p}} = \frac{\rho\,(K - \hat{R}_{\rm cp})\,(1 + h_{\rm rc}\, a_{\rm rc}\, \hat{R}_{\rm cp})\, a_{\rm cp} - e_{\rm rc}\, a_{\rm rc}\, a_{\rm rp}\, \hat{R}_{\rm cp}^2 + \mu_{\rm c}\,(1 + h_{\rm rc}\, a_{\rm rc}\, \hat{R}_{\rm cp})\, a_{\rm rp}\, \hat{R}_{\rm cp}}{a_{\rm rc}\, \hat{R}_{\rm cp}}\,, \tag{A4}$$

which we can write as a quadratic equation in $\hat{R}_{\rm cp}$:

$$\mathcal{A}\, \hat{R}_{\rm cp}^2 + \mathcal{B}\, \hat{R}_{\rm cp} + C = 0\,, \tag{A5}$$

with

$$\begin{aligned} \mathcal{A} &= a_{\rm rc}\, \left[(e_{\rm cp} - h_{\rm cp}\, \mu_{\rm p})\,(\,\rho\, h_{\rm rc}\, a_{\rm cp} + (e_{\rm rc} - h_{\rm rc}\, \mu_{\rm c})\, a_{\rm rp}\,) - (e_{\rm rp} - h_{\rm rp}\, \mu_{\rm p})\, a_{\rm rp}\right]\,, \\ \mathcal{B} &= a_{\rm rc}\, \mu_{\rm p} + (e_{\rm cp} - h_{\rm cp}\, \mu_{\rm p})\,(\,\rho\,(1 - K\, h_{\rm rc}\, a_{\rm rc})\, a_{\rm cp} - a_{\rm rp}\, \mu_{\rm c}\,)\,, \\ C &= -\rho\, K\,(e_{\rm cp} - h_{\rm cp}\, \mu_{\rm p})\, a_{\rm cp}\,. \end{aligned} \tag{A6}$$

Hence, there are up to two solutions for the equilibrium resource density $\hat{R}_{\rm cp}$ and, likewise, for the consumer–predator equilibrium.

Appendix B Invasion Criteria

Predator in Consumer Equilibrium

Invasion by the predator into the consumer equilibrium will be possible if the growth rate of the predator in the consumer equilibrium is > 0 when the predator density is very small but positive. If we divide the right-hand side of equation (1) by P and require the result to be positive, we obtain the following criterion:

$$\frac{e_{\rm rp}\, a_{\rm rp}\, \hat{R}_{\rm c} + e_{\rm cp}\, a_{\rm cp}\, \hat{C}_{\rm c}}{1 + h_{\rm rp}\, a_{\rm rp}\, \hat{R}_{\rm c} + h_{\rm cp}\, a_{\rm cp}\, \hat{C}_{\rm c}} - \mu_{\rm p} > 0\,. \tag{B1}$$

Substituting $\hat{R}_{\rm c}$ and $\hat{C}_{\rm c}$ from equation (4) and rearranging yields the criterion for successful invasion by the predator into the consumer equilibrium:

$$a_{\rm cp} > \frac{a_{\rm rc}\, \mu_{\rm p}\,(e_{\rm rc} - h_{\rm rc}\, \mu_{\rm c}) - a_{\rm rp}\, \mu_{\rm c}\,(e_{\rm rp} - h_{\rm rp}\, \mu_{\rm p})}{\rho\, e_{\rm rc}\,(K\, a_{\rm rc}\,(e_{\rm rc} - h_{\rm rc}\, \mu_{\rm c}) - \mu_{\rm c})(e_{\rm cp} - h_{\rm cp}\, \mu_{\rm p})}\, \mu_{\rm c}\,. \tag{B2}$$

Neutrality of this condition defines K_{BP_2} in figure 2 and curve C_{BP_2} in figure 3.

Consumer in Predator Equilibrium

Invasion by the consumer into the predator equilibrium will be possible if the growth rate of the consumer in the predator equilibrium is > 0 when the consumer density is very small but positive. If we divide the right-hand side of equation (2) by C and require the result to be positive, we obtain the following criterion:

$$\frac{e_{\mathrm{rc}}\, a_{\mathrm{rc}}\, \hat{R}_{\mathrm{p}}}{1 + h_{\mathrm{rc}}\, a_{\mathrm{rc}}\, \hat{R}_{\mathrm{p}}} - \frac{a_{\mathrm{cp}}\, \hat{P}_{\mathrm{p}}}{1 + h_{\mathrm{rp}}\, a_{\mathrm{rp}}\, \hat{R}_{\mathrm{p}}} - \mu_{\mathrm{c}} \;>\; 0\,. \tag{B3}$$

[Notice that we can neglect the term $h_{\mathrm{cp}}\, a_{\mathrm{cp}}\, C$ in the denominator of the predator's consumption rate in eq. (2), because C is very small.] Substituting $\hat{R}_{\mathrm{p}}$ and $\hat{P}_{\mathrm{p}}$ from equation (5) and rearranging yields the criterion for successful invasion by the consumer into the predator equilibrium:

$$a_{\mathrm{cp}} \;<\; \frac{a_{\mathrm{rp}}\, \mu_{\mathrm{p}}}{\rho\, (K\, a_{\mathrm{rp}}\, (e_{\mathrm{rp}} - h_{\mathrm{rp}}\, \mu_{\mathrm{p}}) - \mu_{\mathrm{p}})} \left(\frac{e_{\mathrm{rc}}\, a_{\mathrm{rc}}\, \mu_{\mathrm{p}}}{a_{\mathrm{rp}}\, (e_{\mathrm{rp}} - h_{\mathrm{rp}}\, \mu_{\mathrm{p}}) + h_{\mathrm{rc}}\, a_{\mathrm{rc}}\, \mu_{\mathrm{p}}} - \mu_{\mathrm{c}} \right). \tag{B4}$$

Neutrality of this condition defines K_{BP_3} in figure 2 and curve C_{BP_3} in figure 3.

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