

Modeling direct positive feedback between predators and prey

David H. Brown,^{a,*} Howard Ferris,^b Shenglei Fu,^b and Richard Plant^a

^aDepartment of Agronomy and Range Science, University of California, Davis, One Shields Avenue, Davis, CA 95616-8633, USA

^bDepartment of Nematology, University of California, Davis, USA

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Abstract

Predators can have positive impacts on their prey through such mechanisms as nutrient mineralization and prey transport. These positive feedbacks have the potential to change predictions based on food web theory, such as the assertion that enrichment is destabilizing. We present a model of a simple food web, consisting of a resource, a consumer, and its predator. We assume that the predator has a direct positive effect on the consumer, by increasing the rate at which the consumer acquires resources. We consider two cases: the feedback strength is a saturating function of predator density, or it is proportional to the encounter rate between predators and prey. In both cases, the positive feedback is stabilizing, delaying or preventing the onset of oscillations due to enrichment. Positive feedback can introduce an Allee effect for the predator population, yielding multiple stable equilibria. Strong positive feedback can yield counterintuitive results such as a transient increase in consumer density following the introduction of predators, and a decrease in the resource pool following enrichment.

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1. Introduction

The basic building block of food web models is the predator–prey interaction. Encounters between predators and prey are assumed to result in an increased predator biomass and a decreased prey biomass, and predators are usually assumed to have a purely negative effect on their prey. However, a number of studies have demonstrated that predators can also have positive effects on their prey (Bianchi and Jones, 1991; Diehl et al., 2000; Ingham et al., 1985; Verhoef and Brussaard, 1990). Proposed mechanisms for positive feedback from predators to their prey include the ability of predators to mineralize nutrients limiting to the prey or to their resource (DeAngelis, 1992), transport the prey to locations with unexploited resources (Ingham et al., 1985), increase resource accessibility or palatability (Seastedt, 1984; Verhoef and Brussaard, 1990), change the prey's foraging behavior (Peacor, 2002), and return biomass to the resource pool as detritus (DeAngelis, 1992). Predators can also have indirect positive effects on their prey by consuming the prey's competitors or

other predators (Abrams, 1992). Positive feedbacks can alter relationships at the core of food webs, and thus are likely to have profound effects on many aspects of food web structure, function, and dynamics (Bianchi et al., 1989; Bengtsson et al., 1996; DeAngelis et al., 1986; DeAngelis, 1992; Stone and Weisburd, 1992).

These proposed mechanisms of positive feedback have received different levels of empirical support and theoretical development. The most thoroughly studied mechanism is that of nutrient cycling, in which carbon-limited predators mineralize excess nutrients (typically nitrogen or phosphorous), making it available for lower trophic levels. Examples of this include unglulates (predators) grazing on plants (prey) (e.g. McNaughton, 1984), sea urchins and *Daphnia* feeding on algae (Carpenter, 1986; Porter, 1976; Sterner, 1986), and soil fauna feeding on microbes (Bengtsson et al., 1996; Lussenhop, 1992; Verhoef and Brussaard, 1990). A number of models have been developed to determine the theoretical implications of nutrient cycling in predator–prey systems. For example, intermediate levels of grazing by herbivores can increase plants' primary productivity (de Mazancourt et al., 1998). The destabilizing effects of nutrient enrichment (Rosenzweig, 1971) may be enhanced by the return of nutrients

*Corresponding author. Fax: 530-752-4906.

E-mail address: dhbrown@ucdavis.edu (D.H. Brown).

through the detrital pathway from predators to their prey (DeAngelis, 1992).

Not all positive feedback between predators and prey is mediated by nutrient cycling, however. Predators can have a direct positive effect on their prey's ability to acquire resources through several mechanisms. Predators can transport prey to areas of unexploited resources (Ingham et al., 1985), or make resources more accessible by altering the physical structure of the environment (Moore et al., 1988; Rice, 1986). The most thoroughly studied example of direct positive feedback is that of granivores, which can enhance seedling recruitment by dispersing or caching seeds (e.g. Brown et al., 1979; Longland et al., 2001). Another important example is the relationship between soil bacteria and their nematode predators. A significant portion of the bacteria ingested by nematodes pass through the gut and are returned to the soil unharmed (Killham, 1994). By transporting bacteria and inoculating unexploited resource pools, nematodes may play an important role in speeding decomposition (Ingham et al., 1985). The combination of direct and nutrient-mediated positive effects of bacterial-feeding nematodes can be sufficiently strong that bacterial populations are sometimes greater in the presence of these predators than in their absence (Abrams and Mitchell, 1980; Gould et al., 1981; Ingham et al., 1985; Trofymow et al., 1983). In a short term microcosm experiment, Fu et al. (submitted) estimated that two species of bacterial-feeding nematodes, *Cruz-nema tripartitum* and *Acrobeloides bodenheimeri*, increased the rate at which soil bacteria acquired resources by factors of 15 and 5–10, respectively. In general, the net impact of predators on their prey will depend on the balance between positive and negative effects; we speak of positive feedback occurring whenever the prey's per capita feeding rate increases with predator density.

While detailed models of the positive effects of granivory have been studied for some systems (Vander Wall, 1993), there has not been an attempt to develop a general theory of direct positive feedback comparable to that of nutrient cycling. Toward this end, we present a model incorporating direct positive feedback between a predator and its prey. We model a simple food chain, consisting of a resource, its consumer, and the consumer's predator. We assume that the predator has a positive effect on the rate at which the consumer acquires its resource. We consider two possible cases: either the strength of the positive feedback is a saturating function of predator density, or it is proportional to the encounter rate between predators and consumers. We structure the analysis around two questions:

1. What is the effect of adding predators to the predator-free system?

2. How does the system respond to enrichment, i.e. an increase in the supply rate of the basal resource?

We also examine the implications of the strength of coupling between the predator and consumer populations by studying the behavior of the model with the predator density fixed by external factors.

We are motivated by a desire to understand the role of bacterial-feeding nematodes in ecosystem processes, so the model structure and parameter values are tuned to this system. However, we believe that the model is general enough to offer insight into universal features of direct positive feedback between predators and prey. Our results may also serve as a guide for understanding the positive effects of granivory, by interpreting the "consumers" to be plants, and their resource to be a limiting nutrient or space (we do not usually speak of the rate at which plants "feed" on such resources, but the phenomena of resource acquisition are analogous). By dispersing seeds or facilitating germination, granivores can accelerate the rate at which plants acquire these resources, much as a nematode can transport bacteria to unexploited resource pools. Of course, a granivore–plant–resource system differs in important ways from a simple predator–prey–resource food chain, since granivores mediate plants' reproduction rather than removing individual prey. Other important factors include seed caching behaviors and the mode of resource acquisition by the plants. A model as general as ours serves as a point of departure so that differences between systems can be understood within a theoretical framework.

2. Model structure

We formulate a dynamic model with three components: a resource (\hat{R}), its consumer (\hat{C}), and the consumer's predator (\hat{P}), each measured in biomass per unit area or volume. We assume that the resource is supplied at a constant rate, r , and decays at a constant rate, n . In soil food webs, for example, the resource consists primarily of organic matter deposited by plants; we assume that the rate of deposition is approximately constant on the timescale relevant to the food web's dynamics. We do not incorporate any density dependence in the resource dynamics, assuming that the resource supplier is at an equilibrium determined by factors outside the scope of the model. The resource becomes unavailable to the consumer at rate n due to transport, physical or chemical changes, or consumption by other consumer populations. We assume that the consumer acquires the resource at a per capita rate $F_1(\hat{R})$, converting resource biomass to consumer biomass with an assimilation/production efficiency $b_1 \leq 1$; the consumer has a density-independent death rate of

m_1 . Similarly, the predator feeds on the consumer at a per capita rate of $F_2(\hat{C})$, with an assimilation/production efficiency b_2 and a death rate m_2 .

We incorporate direct positive feedback by assuming that the rate at which the consumer acquires resources may be increased by some function of the predator and consumer densities, $G(\hat{P}, \hat{C})$. With these assumptions, the dynamics of the resource, consumer, and predator are governed by the differential equations:

$$\frac{d\hat{R}}{dt} = r - n\hat{R} - \hat{C}F_1(\hat{R})(1 + G(\hat{P}, \hat{C})), \quad (1)$$

$$\frac{d\hat{C}}{dt} = b_1\hat{C}F_1(\hat{R})(1 + G(\hat{P}, \hat{C})) - m_1\hat{C} - \hat{P}F_2(\hat{C}), \quad (2)$$

$$\frac{d\hat{P}}{dt} = b_2\hat{P}F_2(\hat{C}) - m_2\hat{P}. \quad (3)$$

The model is completed by the specification of the functions F_i and G . To keep the analysis as simple as possible, we mainly use linear functional responses for feeding: $F_1(\hat{R}) = a_1\hat{R}$ and $F_2(\hat{C}) = a_2\hat{C}$. However, we are interested in the potentially destabilizing effects of enrichment: increasing the availability of resources can cause a predator–prey system to shift from an equilibrium to oscillations (Rosenzweig, 1971). This “paradox of enrichment” requires saturating functional responses. Thus, we study the effects of enrichment using type II (Holling) functional responses: $F_1(\hat{R}) = \frac{a_1\hat{R}}{1+a_1h_1\hat{R}}$ and $F_2(\hat{C}) = \frac{a_2\hat{C}}{1+a_2h_2\hat{C}}$, where h_i represent prey handling times. Note that these include the linear functional responses as a special case, by setting $h_i = 0$.

The strength of the positive feedback, $G(\hat{P}, \hat{C})$ may depend in a number of ways on the predator and consumer densities, depending on the mechanisms involved. We consider two special cases. In the first, we assume that the feedback strength is a saturating function of the predator’s density alone: $G(\hat{P}) = \frac{g_1\hat{P}}{1+g_1k\hat{P}}$. That is, we assume that the consumer’s feeding rate increases with the density of predators, asymptotically approaching a maximum factor of $1 + \frac{1}{k}$. In the second case, we assume that the feedback depends on the encounter rate between predators and prey. For simplicity, we assume that the feedback is proportional to the predator’s feeding rate: $G(\hat{P}, \hat{C}) = g_2\hat{P}F_2(\hat{C})$. This corresponds more closely to the mechanism of prey transport, while the first case provides a more general, phenomenological approach. We will refer to these two cases as predator-dependent and encounter-dependent feedback, respectively.

Next, we nondimensionalize the equations by rescaling time and biomass. We define $\tau = m_1t$, so that one time unit corresponds to the expected lifespan of the consumer. We define $R = \frac{a_1}{m_1}\hat{R}$, $C = \frac{a_1}{m_1}\hat{C}$, and $P = \frac{a_1}{m_1}\hat{P}$. In order to interpret this rescaling, notice that the

dynamics of the consumer in the predator’s absence are given by

$$\frac{dC}{d\tau} = C\left(\frac{R}{1 + \theta_1 R} - 1\right),$$

where θ_1 is the rescaled handling time (Table 1). Thus, the consumer population will achieve an equilibrium when the resource pool contains $\frac{1}{1-\theta_1}$ units of biomass. The definitions for the nondimensional parameters and the default values that we use, chosen to represent bacterial–nematode interactions in the soil food web (Darrah, 1991; Moore et al., 1996; Ferris et al., 1997), are given in Table 1. The nondimensionalized equations are now

$$\frac{dR}{d\tau} = \rho - vR - \frac{CR}{1 + \theta_1 R}(1 + G(P, C)), \quad (4)$$

$$\frac{dC}{d\tau} = \frac{\beta_1 CR}{1 + \theta_1 R}(1 + G(P, C)) - C - \frac{\alpha PC}{1 + \alpha\theta_2 C}, \quad (5)$$

$$\frac{dP}{d\tau} = \frac{\beta_2 \alpha PC}{1 + \alpha\theta_2 C} - \mu P. \quad (6)$$

After nondimensionalizing, the predator-dependent feedback has the form $G(P) = \frac{\gamma_1 P}{1 + \gamma_1 \kappa P}$, and the encounter-dependent feedback has the form $G(P, C) = \gamma_2 P F_2(C)$. Throughout the analysis, we restrict ourselves to linear functional responses ($\theta_i = 0$) unless otherwise stated.

Table 1
Nondimensional parameter definitions and default values

Resource supply rate	$\rho = \left(\frac{a_1}{m_1}\right)r$	
Resource decay rate	$v = \left(\frac{1}{m_1}\right)n$	
Predator’s feeding rate	$\alpha = \left(\frac{1}{a_1}\right)a_2$	6.0
Predator’s death rate	$\mu = \left(\frac{1}{m_1}\right)m_2$	2.68
Consumer’s assimilation/production efficiency	$\beta_1 = b_1$	0.5
Predator’s assimilation/production efficiency	$\beta_2 = b_2$	0.22
Consumer’s handling time	$\theta_1 = m_1 h_1$	0.005
Predator’s handling time	$\theta_2 = m_1 h_2$	0.01
Predator–dependent feedback strength	$\gamma_1 = \left(\frac{m_1}{a_1}\right)g_1$	
Encounter–dependent feedback strength	$\gamma_2 = \left(\frac{m_1}{a_1}\right)^2 g_2$	
Predator–dependent feedback saturation	$\kappa = k$	

3. Results

3.1. General features

We begin by describing several features of the model which are independent of the type of feedback. In the absence of the predator, the resource and consumer converge to a stable equilibrium, $R_0 = \frac{1}{\beta_1}$ and $C_0 = \beta_1\rho - v$ (note that we require $\beta_1\rho > v$ for the consumer to survive). Since the resource is supplied at a constant rate, the resource isocline in the consumer–resource system is a strictly decreasing function of consumer density. As a result, this model does not allow the phenomenon described by Abrams (1992) in which the elevated consumer mortality caused by predation can in itself have a positive effect on consumer density. If the predator is introduced to the equilibrium system at low density, its population will increase if and only if the invasion criterion $\beta_2\alpha C_0 > \mu$ is satisfied (i.e. it must acquire biomass faster than it loses it). This criterion can also be expressed as

$$\rho > \frac{1}{\beta_1} \left(v + \frac{\mu}{\beta_2\alpha} \right) = \rho_c. \tag{7}$$

Thus, the resource has to be supplied above a critical rate for the predator to survive. This criterion does not depend on the positive feedback, since at arbitrarily low initial densities the predator has no effect on the system.

In the presence of the predator, the consumer reaches an equilibrium found by solving $\frac{dP}{dt} = 0$, yielding

$$C^* = \frac{\mu}{\beta_2\alpha} = \beta_1\rho_c - v. \tag{8}$$

Thus, the top–down regulation of the consumer by predation causes the equilibrium consumer population to be insensitive to the resource supply or feeding rate, and hence to the positive feedback. This insensitivity of the equilibrium consumer biomass to resource availability is a hallmark of trophic cascades (Polis et al., 2000) that occur in simple food-web models with tight coupling of predators and their prey. In addition, since $C_0 - C^* = \beta_1(\rho - \rho_c)$, we see that a successful predator invasion always causes a decrease in the equilibrium consumer population.

If there is no feedback ($\gamma_1 = \gamma_2 = 0$), the system’s equilibrium is given by $R = \frac{\rho}{\beta_1\rho_c}$, and $P = \frac{1}{\alpha}(\frac{\rho}{\rho_c} - 1)$. Thus, enrichment of the system by increasing ρ causes the predator and resource biomasses to increase, but not the consumer’s. When type II functional responses are used, enrichment causes the equilibrium to lose stability via the familiar paradox of enrichment (Rosenzweig, 1971). Increasing ρ causes the system to take longer to return to equilibrium after a perturbation; at a critical value a Hopf bifurcation occurs, with the stable equilibrium giving way to stable oscillations that grow in amplitude with ρ (Fig. 1).

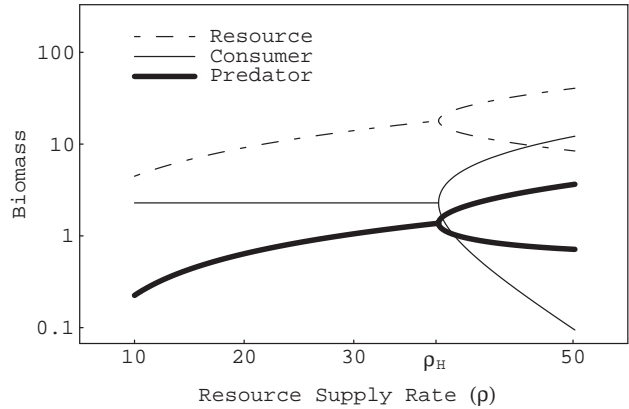


Fig. 1. Destabilizing effect of enrichment with no feedback. As the supply rate increases, the equilibrium gives way to periodic oscillations (high and low values are plotted).

3.2. Equilibria

We begin with predator–dependent feedback $G(P) = \frac{\gamma_1 P}{1 + \gamma_1 \kappa P}$. The resource and predator equilibria are given by

$$R^* = \frac{1}{v} \left(\rho - \frac{C^*}{\beta_1} (1 + \alpha P^*) \right), \tag{9}$$

$$P^* = \frac{\Delta \pm \sqrt{\Delta^2 + 4\alpha\gamma_1(C^*(1 + \kappa) + \kappa v)(C_0 - C^*)}}{2\alpha\gamma_1(C^*(1 + \kappa) + \kappa v)}, \tag{10}$$

where $\Delta = \gamma_1(1 + \kappa)(C_0 - C^*) + v(\gamma_1 - \alpha) - \alpha C^*$. We thus have a pair of nontrivial equilibria provided that $\Delta > 0$ when the discriminant $(\Delta^2 + 4\alpha\gamma_1(C^*(1 + \kappa) + \kappa v)(C_0 - C^*))$ is zero. This requirement can be shown to be equivalent to the condition $(\gamma_1 - \alpha)v > \frac{\mu}{\beta_2}$. Thus, we can have multiple equilibria if and only if the feedback is sufficiently strong and the resource decays sufficiently fast. In this case, a saddlenode bifurcation gives rise to a pair of nontrivial equilibria (one stable and one unstable) that coexist with the stable zero equilibrium over a range of values of ρ (Fig. 2); above ρ_c only the stable branch remains positive. This situation acts much like an Allee effect (Allee, 1931): in the region of bistability, the predator can maintain itself at high enough density via the positive feedback, but it cannot increase from low levels. The higher consumer feeding rate due to feedback can only make the difference between the persistence and extinction of the predator if the resource decays quickly enough. While the feedback saturation constant κ does not enter the criterion for bistability, it does affect the range of resource supply rates over which the multiple equilibria coexist. Note that in the region of bistability, the consumer population is greater when predators are present than when they are absent. If the condition for bistability is not met, the trivial equilibrium loses stability via a transcritical bifurcation at $\rho = \rho_c$.

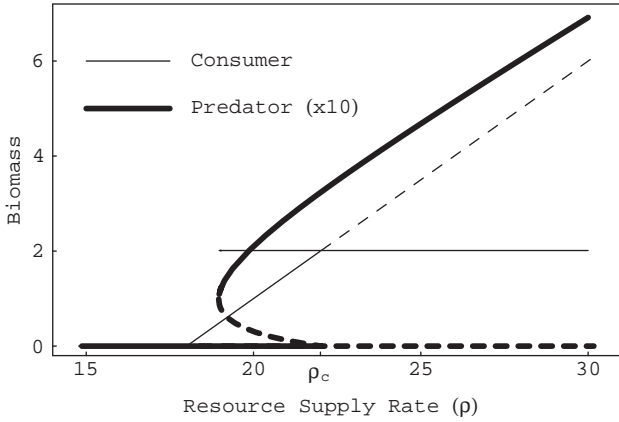


Fig. 2. Bistability due to predator–dependent feedback: stable zero and nonzero predator equilibria coexist over a range of resource supply rates below ρ_c . Solid lines indicate stable equilibria; dashed lines indicate unstable equilibria. Non–default parameter values are: $\gamma_1 = 13$ and $v = 9$.

If the feedback is proportional to the encounter rate ($G(P, C) = \gamma_2 \alpha PC$), the equilibria are given by

$$R^* = \frac{1}{v} \left(\rho - \frac{C^*}{\beta_1} (1 + \alpha P^*) \right), \quad (11)$$

$$P^* = \frac{\Delta \pm \sqrt{\Delta^2 + 4\gamma_2 C^{*2} (C_0 - C^*)}}{2\alpha\gamma_2 C^{*2}}, \quad (12)$$

where $\Delta = \gamma_2 C^* (C_0 - C^* + v) - (C^* + v)$. Again we have the possibility of multiple nontrivial equilibria; here, the condition for bistability is $(\gamma_2 \mu - \alpha \beta_2) v > \mu$. As before, bistability occurs if and only if the feedback is sufficiently strong and the resource decays quickly enough.

For both types of feedback, we have seen that the predator population can increase from arbitrarily low density if and only if the resource supply rate is above a threshold; the invasion then leads to a lower consumer biomass. The predator can have a positive effect on consumer biomass only under the conditions of bistability, whereby it maintains itself at a nontrivial density even if the resource supply rate is below the threshold. However, experimental evidence suggests that the introduction of predators can cause an increase in prey biomass more robustly than our results indicate (Abrams and Mitchell, 1980; Gould et al., 1981; Trofymow et al., 1983; Ingham et al., 1985). Our predictions are governed by the top–down structure of the model, in which the predator’s density is limited only by the availability of prey. In order to relax this assumption, we next partially decouple the predator and consumer populations by assuming that the predator population is fixed by factors other than prey availability.

3.3. Fixed predator population

A predator population whose level is not tightly coupled to prey availability may arise in several ways. It may be the result of other sources of density dependence, or of experimental manipulation. Alternatively, if the dynamics of the predators are significantly slower than those of the consumer, the predator population may be approximately constant over timescales relevant to consumer–resource dynamics. Inactive life stages, such as dauer larvae in some nematodes (Riddle, 1988), may act to buffer predator populations against fluctuations in prey availability. To model these situations, we fix the predator population at an arbitrary level, P_f , and consider the dynamics of the consumer–resource subsystem. This partial decoupling of the predator and consumer densities represents an alternative to strict top–down control, without invoking a particular mechanism.

With predator–dependent positive feedback, a fixed predator population yields a unique stable equilibrium:

$$R^* = (1 + \alpha P_f) \frac{1 + \gamma_1 \kappa P_f}{1 + \gamma_1 (1 + \kappa) P_f} R_0, \quad (13)$$

$$C^* = \frac{\beta_1 \rho}{1 + \alpha P_f} - \frac{v(1 + \gamma_1 \kappa) P_f}{1 + \gamma_1 (1 + \kappa) P_f}. \quad (14)$$

The requirement that C^* be nonnegative places an upper limit on the possible predator population. We now ask whether the addition of predators can increase the consumer population over the predator–free levels. While sufficiently high predator density always leads to a decrease in the consumer population, the consumers may increase under low levels of predation (Fig. 3). This positive response to the addition of predators occurs if $\left. \frac{dC^*}{dP_f} \right|_{P_f=0} > 0$, which is equivalent to $\gamma_1 > \frac{\beta_1 \rho \alpha}{v}$. Moreover, we find that $C^* > C_0$ if and only if $\gamma_1 [v - \alpha P_f (\beta_1 \rho (1 + \kappa) - v)] > \alpha \beta_1 \rho$. Thus, introducing predators causes the consumer population to increase provided that the feedback is strong enough, the resource decays quickly enough, and the predator population and feedback saturation parameter are not too large. This may be observed as a transient phenomenon before the predator’s population equilibrates, or it may be permanent if factors other than prey availability limit the predator’s population.

With encounter–dependent feedback, the effects of introducing a fixed predator population are more complex. In this case, the resource and consumer equilibria are given by

$$R^* = \frac{1}{v} \left(\rho - \frac{C^*}{\beta_1} (1 + \alpha P_f) \right), \quad (15)$$

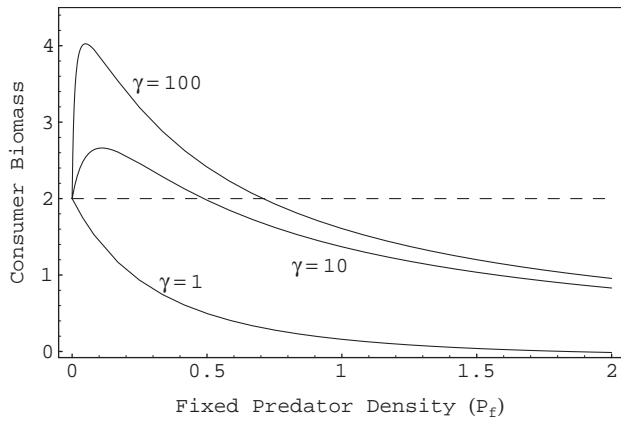


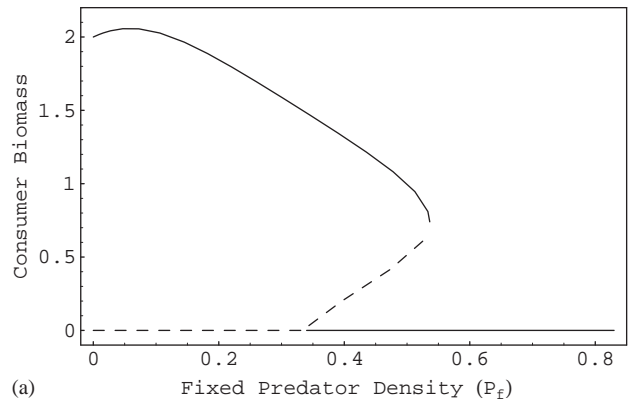
Fig. 3. Effects of predator–dependent feedback with a fixed predator density: low predator numbers with strong positive feedback can cause an increase in the equilibrium consumer density. Parameters are: $\alpha = 2, \rho = 10, v = 3, \kappa = 0.01$.

$$C^* = \frac{\Delta \pm \sqrt{\Delta^2 + 4\gamma_2\alpha P_f(\alpha P_f + 1)(\beta_1\rho - v(\alpha P_f + 1))}}{2\gamma_2\alpha P_f(\alpha P_f + 1)}, \tag{16}$$

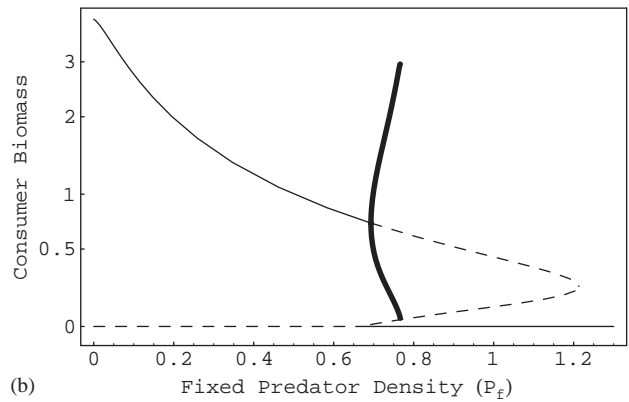
where $\Delta = \beta_1\rho\gamma_2\alpha P_f - (\alpha P_f + 1)$. There are two cases. If $\gamma_2 < \frac{1}{\beta_1\rho - v}$, then there is a single positive equilibrium which loses stability to the trivial equilibrium via a transcritical bifurcation at $P_f = \frac{\beta_1\rho - v}{\alpha v}$. If $\gamma_2 > \frac{1}{\beta_1\rho - v}$, then two nontrivial equilibria coexist over a range of predator levels. In this case, we either have bistability once again (Fig. 4a) or the stable equilibrium undergoes a Hopf bifurcation, with the periodic orbit destroyed via a homoclinic bifurcation (Fig. 4b). Thus, under conditions of strong encounter–dependent feedback, the introduction of a fixed predator population may induce oscillations in the consumer population. The introduction of predators can also lead to a higher equilibrium consumer population. Solving the inequality $C^* > C_0$ leads to the condition: $\gamma_2(\beta_1\rho - v)[v(\alpha P_f + 1) - \beta_1\rho\alpha P_f] > \beta_1\rho$. As before, this requires that the feedback is strong enough, the resource decays quickly enough, and the predator population is not too large. Moreover, this condition implies that $\gamma_2 > \frac{1}{\beta_1\rho - v}$, so that the addition of predators can cause the consumer population to increase only in the case that further predator additions will lead to multiple equilibria.

3.4. Enrichment and the resource pool

Returning to the full model (the predator population is not fixed), we now turn our attention to the effects of enrichment, i.e. increasing ρ , the supply rate of the basal resource. We are interested in two responses to enrichment: the size of the resource pool, and the stability of the system. Intuitively, one would expect the size of the resource pool to grow when the supply rate increases. However, enrichment in soil systems often



(a)



(b)

Fig. 4. Effects of encounter–dependent feedback with a fixed predator density. (a) Bistability, with $\alpha = 2, \rho = 10, v = 3, \gamma_2 = 1$. (b) Homoclinic bifurcation (heavy line denotes periodic orbit), with $\alpha = 6, \rho = 10, v = 1, \gamma_2 = 1$.

leads to a “priming effect”, in which there is a net loss of soil carbon after the input of organic matter (Fu and Cheng, 2002; Kuzyakov, 2002). There are several possible mechanisms for such priming effects, including heightened microbial activity in response to easily metabolized carbon sources. Since microbial predators may play an important role in inducing the priming effect (Henkinet et al., 1990), we are interested in determining whether this may be a result of direct positive feedback.

For our purposes, we will define a priming effect to exist if the size of the resource pool decreases when the supply rate increases: $\frac{dR^*}{d\rho} < 0$. When this occurs, the input of additional resources facilitates the consumption of resources already present. With predator–dependent feedback and linear functional responses, solving this inequality leads to the condition:

$$\begin{aligned} \alpha C^{*2}(\gamma_1 - \alpha) &> \kappa[\gamma_1^2(1 + \kappa)^2(C_0 - C^*)^2 + v^2(\gamma_1 - \alpha)^2 \\ &\quad - (2v + C^*)(\gamma_1 - \alpha)\alpha C^* \\ &\quad + 2\gamma_1(v(\gamma_1 - \alpha) + \alpha C^*)(1 + \kappa)(C_0 - C^*) \\ &\quad + 4\alpha\gamma_1\kappa v(C_0 - C^*)]. \end{aligned}$$

In the special case that the feedback is not saturating ($\kappa = 0$), this condition reduces to $\gamma_1 > \alpha$. More generally,

there is a priming effect if the feedback is above a threshold level that depends on the saturation constant and resource supply and decay rates (Fig. 5).

With encounter-dependent feedback, $\frac{dR^*}{d\rho} < 0$ if and only if $\gamma_2 > \frac{\beta_2 z}{\mu}$. As before, we find a priming effect if the feedback is sufficiently strong. Here, however, the threshold level of feedback does not depend on the resource decay rate. In addition, since $\frac{dR^*}{d\rho}$ is not a function of ρ , the resource pool is either a strictly increasing or decreasing function of the supply rate.

Both forms of direct positive feedback are capable of producing the counterintuitive result that enrichment may lead to a smaller resource pool. An increased resource supply rate yields a higher predator population; with sufficiently strong positive feedback, this causes the consumer’s feeding rate to increase enough that there is a net decrease in the resource pool.

3.5. Enrichment and stability

Finally, we consider how direct positive feedback influences the destabilizing effects of enrichment. With

type II functional responses for predation, there is a critical resource supply rate, ρ_H , at which the system undergoes a Hopf bifurcation (Fig. 1). An intuitive explanation for this “paradox of enrichment” is as follows: high levels of predation cause the consumer population to decline. This is followed by a decline in the predator population due to the lack of sufficient prey. During this phase, the resource pool grows because of the scarcity of consumers and their saturating functional response. The consumer population then finds itself with ample resources and few predators, allowing it to grow rapidly. The low predator population cannot check this growth initially, because of its saturating functional response, thus allowing both consumer and predator populations to reach high levels, inducing the next crash. Enrichment is destabilizing because it causes the resource pool to grow more rapidly, fueling more violent boom and bust cycles.

In Fig. 6, we plot ρ_H as a function of the feedback parameters. Predator-dependent feedback is always stabilizing, since it shifts the onset of oscillations to higher resource supply rates. In fact, it appears that when the feedback is sufficiently strong, no level of resource supply can destabilize the system. This stabilizing effect is mitigated by the saturation of the feedback; as the feedback saturates at lower predator populations, it has less of an effect on stability. Intuitively, the feedback is stabilizing because during a period of declining consumer density, the presence of predators (whose decline lags behind) increases the feeding rate of consumers. This allows the consumers to acquire resources more efficiently, slowing their decline and preventing the buildup of a large resource pool which would fuel explosive growth of the consumer population.

While encounter-dependent feedback is also strongly stabilizing at high levels, it is destabilizing at low levels: the presence of weak encounter-dependent feedback lowers the critical resource supply rate ρ_H . While

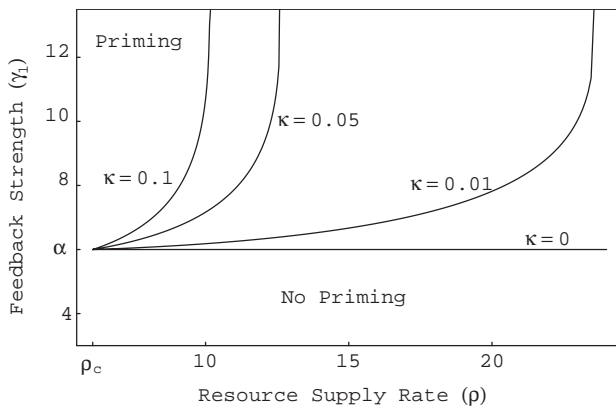


Fig. 5. Priming effect induced by predator-dependent feedback. Above each curve, increasing the resource supply rate causes the resource pool to shrink ($v = 1.0$).

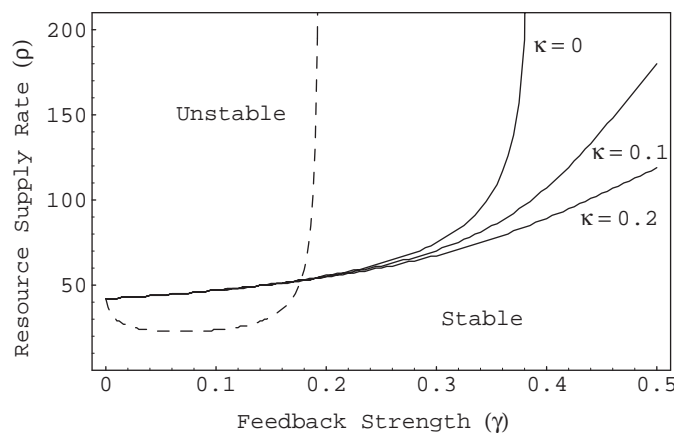


Fig. 6. Stabilizing effects of positive feedback: curves indicate the resource supply rate at which oscillations begin. Solid curves represent predator-dependent feedback; dashed curve represents encounter-dependent feedback ($v = 0.1$).

feedback helps keep the size of the resource pool in check, it also allows the consumer population to grow more rapidly with a given level of resources. Thus, there is a tradeoff between stabilizing and destabilizing effects, and the net result shifts from destabilizing to stabilizing as the feedback strength increases. The destabilizing effects are manifested only when feedback depends on the density of consumers, which helps the growth of consumers to fuel further growth.

4. Discussion

There is growing evidence that treating predation as a purely extractive process is incomplete (Abrams, 1992; Bengtsson et al., 1996; Bianchi et al., 1989; Bianchi and Rice, 1988; Ingham et al., 1985). By mineralizing nutrients, transporting prey and their resources, or altering prey behavior, predators can have positive effects on lower trophic levels. While the role of nutrient mineralization has been modeled extensively, more direct forms of feedback such as prey transport have received little attention from theorists. To shed some light on this subject, we have analyzed a simple food-web model in which the feeding rate of a consumer increases as a function either of its predator's density or of the predator–consumer encounter rate.

Incorporating direct positive feedback from the predator to the consumer alters several aspects of the food web's dynamics. First, feedback can induce an Allee effect, in which the predator can persist at a high density but not invade from a low one. Second, if the predator density is fixed by factors other than prey availability, positive feedback can cause the consumer population to increase above predator-free levels. Third, feedback can cause a priming effect, in which the input of additional basal resources causes the standing resource pool to shrink. Finally, direct positive feedback tends to be stabilizing, delaying or preventing the onset of oscillations with enrichment—although low levels of encounter-dependent feedback are destabilizing.

There are a number of useful extensions of this theory that could be made within the current modeling framework. For example, the strictly top-down structure of our full model ensures that the consumer's equilibrium biomass is not affected by the feedback, and thus does not increase when predators are introduced. However, in most real food webs, consumers are likely to be controlled partially by the availability of resources (Abrams and Walters, 1996; DeAngelis et al., 1996). Several mechanisms can remove this strict top-down control of consumer density, including density dependence in the predator, prey invulnerability (Abrams and Walters, 1996; Elliott et al., 1980), adaptive foraging (Abrams, 1996), and ratio-dependent predation (Arditi

and Michalski, 1996). We relaxed the top-down structure by arbitrarily fixing predator levels; more detailed modeling of these other mechanisms will shed light on when predators can have a net positive effect on their prey's density. In addition, our assumption of a constant resource input rate is a useful approximation for soil food webs and systems with a high degree of allochthonous input, but will be inappropriate for many other systems. If the resource has nontrivial dynamics on the same timescale as the higher trophic levels, this assumption must be modified; they may tend to amplify the effects of positive feedback, damp them out, or introduce new phenomena.

Other extensions of the theory will require substantially different modeling approaches. For example, developing a more mechanistic, detailed understanding of positive feedback through prey transport will require spatially explicit or metapopulation models. It will also be important to study the role of positive feedback in models that more closely approximate the complex topologies of real food webs with many species. It is difficult to predict the extent to which the insights from the simple model will translate directly to more complex food webs. The effects of positive feedback may be damped out by a complex web of interactions, or they may give rise to phenomena not observable in the simple model. Thus, the study of complex topologies with simple types of feedback should complement more mechanistic treatments of feedback in a simple web.

Of course, this theoretical work must be guided and tested by experiments. Relatively little is known about the existence or strength of direct positive feedback in most predator–prey systems. We have been able to quantify the strength of positive feedback in microcosm experiments for two species of bacterial feeding nematodes (Fu et al., submitted). *Cruzema tripartitum* and *Acrobeloides bodenheimeri* were highly effective in dispersing bacteria from an initial inoculum, resulting in resource acquisition rates by the bacteria that were 15 and 5–10 times higher, respectively, in the presence of the nematodes than in their absence. We were not able to determine the dependence of the feedback on nematode density; hence no estimate of the parameters γ_1 or γ_2 is available. Assuming that the feedback was saturated in the experimental systems yields estimates of $\kappa = 0.067$ and 0.1–0.2 for the two species. It remains to be determined how the strength of feedback depends on nematode density, and how strong the effect is over longer temporal and spatial scales. Quantification of feedback strength and identification of the mechanisms involved in other model systems would be extremely useful. Once enough is known to parameterize models for particular systems, the predicted effects of positive feedback must be tested. We have attempted to structure our analysis in a way that is amenable to experimental testing, by focusing on the effects of

predator introduction and resource enrichment, which should be amenable to manipulation in some systems.

We close by mentioning some possible implications of this work for understanding ecosystem functioning. An important environmental issue that may depend critically on positive feedback between predators and prey involves carbon sequestration in soils. Global climate change, with elevated atmospheric CO₂ and temperature, has the potential to increase plants' net primary productivity (Rogers et al., 1994); it has been conjectured that soils may act as a net carbon sink under these conditions, partially offsetting increases in atmospheric CO₂ (Gifford, 1994). The potential of soils to act as a carbon sink is controversial (Canadell et al., 1996; van Kessel et al., 2000); soil carbon sequestration depends on a number of physical, chemical, and management variables (Beran, 1994). At its core, this problem involves the enrichment of a food web with strong positive feedback (Bengtsson et al., 1996; Lussenhop, 1992). By mineralizing nutrients, the soil food web provides positive feedback to plant productivity, thereby increasing the flow of carbon into the soil (DeAngelis, 1992; Setälä and Huhta, 1991; Sulkava et al., 2001; Zak et al., 1993). In contrast, feedback to microbial feeding rate may limit carbon sequestration, as microbes respire more CO₂ back to the atmosphere (Henkinet et al., 1990); we have shown that the carbon pool may actually decrease as the input rate increases, if the feedback is strong. Thus, the carbon storage potential of soils depends critically on the population dynamics and community structure of soil microbes and fauna; positive feedback within this food web is likely an important determinant of ecosystem level carbon fluxes (Cardon, 1996; Cheng, 1999; Hunt et al., 1991; O'Neill, 1994; Parmelee, 1995; Zak et al., 1993).

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