

Transient Dynamics Limit the Effectiveness of Keystone Predation in Bringing about Coexistence

Erik G. Noonburg* and Peter A. Abrams†

Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada

Submitted June 10, 2004; Accepted November 8, 2004;
Electronically published January 20, 2005

Online enhancements: appendixes.

ABSTRACT: We analyze the transient dynamics of simple models of keystone predation, in which a predator preferentially consumes the dominant of two (or more) competing prey species. We show that coexistence is unlikely in many systems characterized both by successful invasion of either prey species into the food web that lacks it and by a stable equilibrium with high densities of all species. Invasion of the predator-resistant consumer species often causes the resident, more vulnerable prey to crash to such low densities that extinction would occur for many realistic population sizes. Subsequent transient cycles may entail very low densities of the predator or of the initially successful invader, which may also preclude coexistence of finite populations. Factors causing particularly low minimum densities during the transient cycles include biotic limiting resources for the prey, limited resource partitioning between the prey, a highly efficient predator with relatively slow dynamics, and a vulnerable prey whose population dynamics are rapid relative to the less vulnerable prey. Under these conditions, coexistence of competing prey via keystone predation often requires that the prey's competitive or antipredator characteristics fall within very narrow ranges. Similar transient crashes are likely to occur in other food webs and food web models.

Keywords: apparent competition, coexistence, competition, diamond food web, mathematical model, transient dynamics.

The role of predators in allowing coexistence of competing prey has been a topic of theoretical and empirical research

* Present address: Centre for Mathematical Biology, Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; e-mail: noonburg@math.ualberta.ca.

† Corresponding author; e-mail: abrams@zoo.utoronto.ca.

Am. Nat. 2005. Vol. 165, pp. 322–335. © 2005 by The University of Chicago. 0003-0147/2005/16503-40484\$15.00. All rights reserved.

since Paine's (1966) well-known study of the effect of sea star predation on the diversity of competing sessile prey species. A keystone predator such as the sea star, *Pisaster ochraceus*, prevents exclusion of the weaker competitor by preferential predation on the stronger competitor. This mechanism is thought to be an important factor maintaining diversity in many natural communities (cf. Mills et al. 1993; Menge et al. 1994; Leibold 1996; Leibold et al. 1997; Chase et al. 2002; Chase and Leibold 2003). For instance, models of keystone predation have figured prominently in analyses of aquatic communities in which two classes of phytoplankton (edible and grazer resistant) share the same essential mineral nutrients and are susceptible to the same set of herbivorous zooplankton (Leibold 1989, 1996; Carpenter 1992; Noonburg et al. 2003; Fox 2004). Indeed, an analysis of several well-studied food webs showed that the "diamond-shaped" pattern of connections, in which competing prey species share both a common resource and a common predator, is one of the most common modules within those larger webs (Milo et al. 2002).

Modeling efforts have focused on describing the conditions under which predator-mediated coexistence is possible (Cramer and May 1972; Phillips 1974; Vance 1974; Armstrong 1979; Leibold 1989, 1996; Carpenter 1992; Abrams 1993, 1999; Holt et al. 1994; Grover and Holt 1998). A necessary condition for stable coexistence of the two prey in the diamond-shaped food web is that they differ in their ratio of sensitivity of per capita growth rate to predator density relative to sensitivity to resource density (Leibold 1996). Roughly speaking, the prey that is the superior resource competitor must be more vulnerable to the predator. This is necessary but not sufficient to produce coexistence. Coexistence also requires that if the prey species are similar in competitive abilities, they cannot differ too much in antipredator abilities (or conversely, similar antipredator abilities mean they cannot differ greatly in competitive ability; Armstrong 1979).

As is true of much ecological theory, studies of coexistence of prey in the diamond food web have often concentrated on equilibrium conditions and conditions for

the increase of species when they are very rare rather than the transient dynamics that precede the limiting behavior (Armstrong 1979; Abrams 1993; Holt et al. 1994; Leibold 1996; Chase and Leibold 2003). However, several studies of other food webs, including those of Hastings and Higgins (1994), Hastings (2001), McCann and Yodzis (1994), and Chen and Cohen (2001), have provided examples of lengthy transients in ecological models (reviewed in Hastings 2004). Transients in at least one model have been shown to entail low densities, which may imply extinction in real systems unless the maximum population sizes are large (Holt and Hochberg 2001). In another example, transient dynamics of the food web have been shown to hide a continual decline in the fitness of one species (Abrams 2002). However, for most simple food webs, we do not know how a consideration of transient dynamics would affect the ecological conclusions normally drawn from those models (Hastings 2004). This article will show that transient cycles with extreme amplitudes characterize a wide range of parameter space in simple models of keystone predation. These transients can greatly reduce the conditions allowing coexistence of prey species in this model and can affect larger food webs that include species that share both predators and limiting resources. The present results suggest that generalist predation may be a less potent mechanism for enabling coexistence between competing prey species than has previously been thought. In particular, such predator-mediated coexistence may be largely restricted to systems based on abiotic resources, to systems with very large population sizes, or to predators whose generation times are not much longer than those of their prey.

In the following “Analysis” section, we begin by considering one of the simplest models of predator-mediated coexistence, a four-species model in which two prey share a single predator and a single resource (the diamond web). We also begin with simple assumptions about the functional and numerical responses of the consumer species. After analyzing the conditions required for coexistence in this model, we then repeat the analysis on a variety of similar but generally more complicated models. The goal in all cases is to determine when transient dynamics significantly restrict the range of prey species characteristics that permit their coexistence.

Analysis

Criteria for Coexistence

It is possible that a diamond-shaped web can arise in a habitat that initially lacks all of the species via simultaneous high levels of immigration of all species. However, when immigration rates are low and all four species are initially

absent, it seems more likely that such a system will be built up one species at a time, starting with the bottom-level species (the resource). To reach the full four-species system, there must then be a feasible sequence of invasions that leads to the full community. In the case considered here, the penultimate step in such an invasion sequence must be a three-species food chain because if the predator is not present, the two prey cannot stably coexist on the single resource (Armstrong and McGehee 1980). There may be one or two different food chains to consider, depending on whether the less vulnerable prey alone can support the predator. If at least one of these invasions is possible, the four-species system can be built up, and coexistence may occur. However, considering only the initial conditions for invasion neglects the dynamics that occur between the initial invasion and the final approach to the equilibrium point. We show below that these dynamics may frequently involve unrealistically low densities of one or more of the component species. Very low densities can imply extinction either because the density represents less than a single individual or because it represents such a small number that either environmental or demographic stochasticity or Allee effects are likely to cause extinction.

Basic Model

Our initial analysis focuses on the simplest model of the diamond food web, in which predator and prey species have linear functional and numerical responses. This web is composed of two competing prey species (with populations N_1, N_2) that share a single resource (R) and a single predator (P). The dynamics are governed by

$$\begin{aligned}\frac{dR}{dt} &= rR\left(1 - \frac{R}{K}\right) - c_1N_1R - c_2N_2R, \\ \frac{dN_1}{dt} &= N_1(b_1c_1R - d_1 - s_1P), \\ \frac{dN_2}{dt} &= N_2(b_2c_2R - d_2 - s_2P), \\ \frac{dP}{dt} &= P(e_1s_1N_1 + e_2s_2N_2 - D).\end{aligned}\tag{1}$$

In the absence of prey (consumers), resource growth is logistic, with intrinsic rate of increase r and carrying capacity K . Each prey species has a type 1 functional response with attack rate c_p , conversion efficiency b_p , and density-independent death at rate d_p . The predator also has a type 1 functional response with attack rate s_p , a conversion efficiency e_p , and a density-independent death rate D . We do not consider type 2 functional responses in this first

model because it is already known that the population cycles that are often generated by such responses significantly narrow the range of prey characteristics allowing coexistence (Abrams 1999), even when transients are not considered.

One condition for coexistence of the two competitors is a trade-off between competitive strength and susceptibility to predation: the superior competitor must be more susceptible to predation. The superior competitor is the species that reduces resource density to the lower equilibrium, that is, the lower R^* in general competition theory (Volterra 1931; Tilman 1982). In the absence of predators, R^* is $d_i/(b_i c_i)$ for competitor i (table 1). Without loss of generality, we assume that N_1 is the superior competitor and N_2 is less vulnerable to predation. In our model, these conditions imply that $d_2/(b_2 c_2) > d_1/(b_1 c_1)$ and $s_2 < s_1$, respectively. Throughout the article, we use d_i as an inverse measure of competitive strength because d_i is proportional to R^* for species i when b and c are fixed. Similarly, we use D (when e is fixed) or D/e as inverse measures of predator efficiency.

Our analysis proceeds as follows. We first present conditions for coexistence of the two competitors at equilibrium in the full four-species system. We then show how these may be modified by the transient dynamics that occur during the process of community assembly.

Conditions for Mutual Invasion

In previous analyses of this type of system, the two prey are considered to coexist if each species is able to increase from low density when the other species are at equilibrium (Abrams 1993; Holt et al. 1994; Leibold 1996; Chase 1999; Chase and Leibold 2003). In general, mutual invasibility need not imply coexistence (Armstrong and McGehee 1980); however, this is true for equation (1) provided there are no restrictions on population size (app. A in the online edition of the *American Naturalist*). We use a superscript to denote the three-species equilibrium with a given prey present; for example, $R^{*(i)}$ is the resource equilibrium when prey species 1 is present but species 2 is absent. Expressions for these equilibria are listed in table 1.

The mutual invasibility conditions partition the parameter space into regions in which competitor 1 excludes competitor 2, competitor 2 excludes competitor 1, or both competitors coexist. As we explain in the next two paragraphs, the diamond community is most likely to be formed by invasion of the food chain with the more vulnerable prey, species 1, by the less vulnerable prey 2. In the following analysis, we present the boundaries in terms of one parameter that determines competitive strength (d_2 ; recall that this is an inverse measure of competitive strength) and another that specifies predator susceptibility

Table 1: Equilibria when one prey species is absent

Predator supported by prey i alone	Predator not supported by prey i alone
$R^{*(i)} = K \left(1 - \frac{c_i D}{r e s_i} \right)$	$R^{*(i)} = \frac{d_i}{b_i c_i}$
$N_i^{*(i)} = \frac{D}{e s_i}$	$N^{*(i)} = \frac{r}{c_i} \left(1 - \frac{d_i}{b_i c_i K} \right)$
$P^{*(i)} = \frac{b_i c_i R^{*(i)} - d_i}{s_i}$	$P^{*(i)} = 0$

Note: i = prey species that is present (see eq. [1]). The condition that prey i alone supports the predator is $(c_i s_i / r c_i) [1 - (d_i / b_i c_i K)] > D$. If the inequality is reversed, the predator is not supported by prey i alone.

(s_2) of species 2 (e.g., fig. 1). For a given value of s_2 , we find the minimum and maximum values of d_2 for which coexistence is possible at equilibrium, and we examine how other parameters influence these boundaries.

Prey species 2 can invade the community consisting of $R^{*(1)}$, $N_1^{*(1)}$, and $P^{*(1)}$ if its per capita growth rate is positive at these densities: $(1/N_2)(dN_2/dt) > 0$. This condition specifies the upper boundary for d_2 :

$$d_2 < b_2 c_2 R^{*(1)} - s_2 P^{*(1)}. \tag{2}$$

The criterion for the lower boundary of d_2 is determined by the invasion condition for species 1 into a food chain with species 2. This condition depends on whether species 2 can support a predator population in the absence of species 1. If species 2 cannot support the predator $P^{*(2)} < 0$ (table 1), species 1 can invade if it outcompetes species 2 in the absence of predators:

$$d_2 > \frac{d_1 b_2 c_2}{b_1 c_1}. \tag{3}$$

Equation (3) defines the minimum d_2 for this case. Invasion of species 1 would then result in exclusion of species 2, and this would eventually be followed by invasion of the predator. The final step in community buildup is then reinvasion of prey 2, which is possible when parameters satisfy inequality (2). However, for some parameters, prey 2 can support a predator population in the absence of prey 1; this occurs if $P^{*(2)} > 0$ (table 1) or

$$d_2 < b_2 c_2 R^{*(2)}. \tag{4}$$

In this case, the minimum value of d_2 is that for which the initial per capita growth rate of a small invading population of species 1 is just positive. This results in the following condition:

$$d_2 > \frac{s_2 d_1}{s_1} + \left(b_2 c_2 - \frac{s_2 b_1 c_1}{s_1} \right) R^{*(2)}. \quad (5)$$

Coexistence boundaries based on mutual invasion are displayed for a sample set of parameter values in figure 1. Figure 1A shows that coexistence can occur over a reasonably broad range of both prey characteristics when the predator is relatively inefficient (high D). Increasing predation on the weaker competitor (increasing s_2) decreases the maximum per capita death rate (d_2) that allows species 2 to invade and therefore decreases the range of d_2 over which coexistence is possible. As shown by comparing the three panels of figure 1, greater predator efficiency (lower D) reduces the range of d_2 , allowing mutual invasion unless the more resistant prey is nearly invulnerable to the predator. When the less vulnerable prey is nearly free of predation ($s_2 \cong 0$), a wide range of d_2 values (i.e., a wide range of relative R^* values for the two prey) allows coexistence regardless of predator efficiency. In fact, when s_2 is close to 0, greater predator efficiency allows coexistence over a wider range of the resource exploitation ability of the second prey (d_2). Rearranging the inequalities so they specify minimum and maximum values of c_2 or b_2 rather than d_2 does not change any of the qualitative results presented here.

Conditions for Invasion Taking Account of Transient Dynamics and Finite Populations

The above analysis does not take into account what happens to both prey and the predator between the initial successful invasion and the final approach to equilibrium densities. Here, we examine these trajectories for a range of parameter values. We determine when large-amplitude transient oscillations follow invasion of the second prey for one or (if two chains are possible) both food chains. If one or more of the three original species drops to an unrealistically low level during these fluctuations, or if the invader itself drops to such a level after its initial period of increase, then the invasion sequence in question will not lead to the full four-species community.

We used numerical integration based on a fourth-order Runge-Kutta algorithm to determine the postinvasion dynamics. We assumed an initial invader density of $N_i = 0.0001$, while the other species start at their equilibrium densities for the three-species chain. Results are relatively insensitive to the initial density of the invader. Figure 2 is an example of such dynamics, showing the large-amplitude oscillations that follow invasion of N_2 . Prey 2 initially depletes the resource, which causes the resident prey (N_1) to decrease because it still suffers relatively high predation as the predator population slowly declines. After the predator

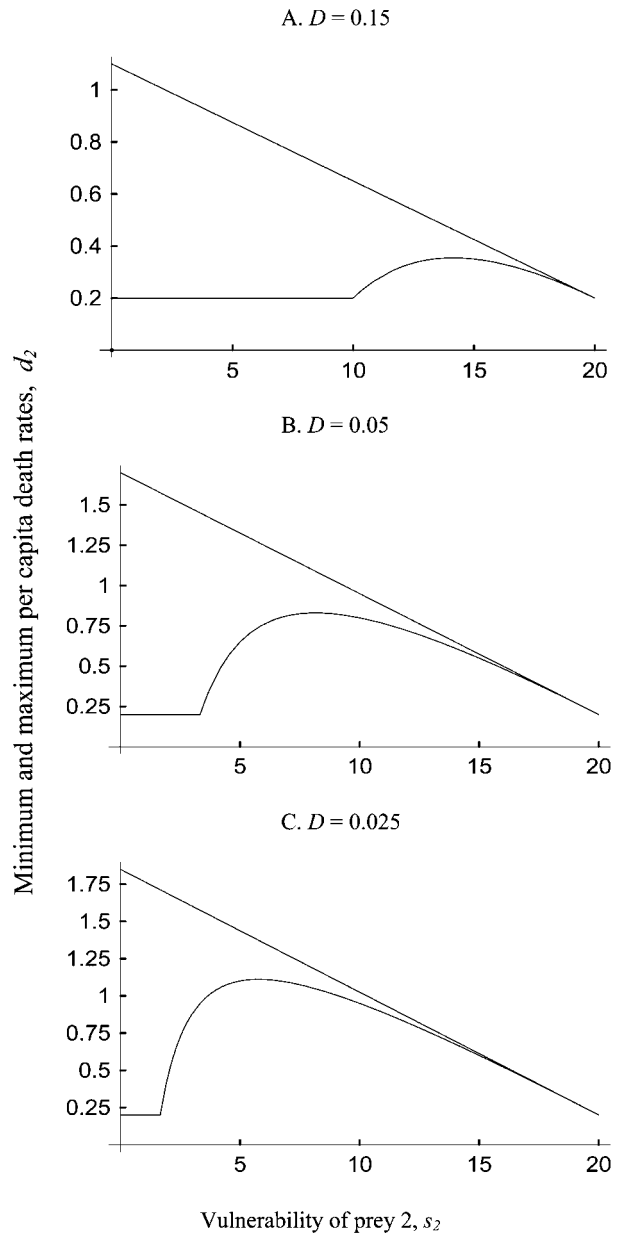


Figure 1: Invasion boundaries determined by inequalities (2)–(5) for three examples differing in the efficiency of the predator as measured by its per capita death rate. The upper and lower lines give the maximum and minimum values of d_2 , the per capita death rate of the less vulnerable prey. The parameter values that are common to all of the panels are $c_1 = 3$, $c_2 = 6$, $b_1 = 1/3$, $b_2 = 1/3$, $d_1 = 0.1$, $r = K = 1$, $e_1 = e_2 = 1/10$, $s_1 = 10$. The boundaries do not take into account the densities of the species at their equilibrium point, provided all densities are positive.

density falls, N_1 recovers and overshoots its new equilibrium, depressing N_2 and thereby perpetuating the cycle. In this example, the minimum density of prey 1 during the initial transient is approximately 3.67×10^{-8} , more

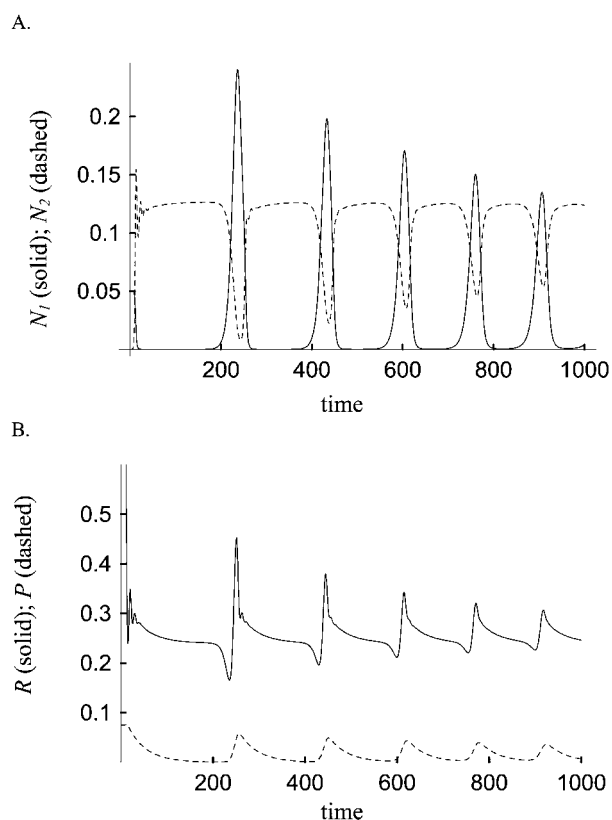


Figure 2: Dynamics of invasion of the three-species community with prey 1 by an inedible prey (N_2). In A, a solid line represents N_1 , and a dashed line represents N_2 . In B, a dashed line represents P , and a solid line represents R . Initial conditions for the three resident species are their equilibrium densities in the absence of N_2 : $R^{*(1)} = 0.85$, $N_1^{*(1)} = 0.05$, $P^{*(1)} = 0.075$. Invasion begins at $t = 0$ with $N_2 = 0.0001$. Parameter values are as follows: $r = 1$, $K = 1$, $c_1 = 3$, $c_2 = 6$, $b_1 = 1/3$, $b_2 = 1/3$, $d_1 = 0.1$, $d_2 = 0.48$, $s_1 = 10$, $s_2 = 2$, $e_1 = 1/10$, $e_2 = 1/10$, $D = 0.05$. The four-species equilibrium is $R^* = 0.2555$, $N_1^* = 0.02799$, $N_2^* = 0.1101$, $P^* = 0.01555$.

than six orders of magnitude below its equilibrium in the food chain lacking prey 2 and almost six orders of magnitude below its eventual equilibrium in the four-species web. This is true even though prey 2 is quite inefficient at resource exploitation (d_2 is more than twice the minimum value for which coexistence at equilibrium is possible).

In the following analysis, we show how consideration of transient dynamics during community buildup narrows the equilibrium coexistence region in figure 1. Oscillations that reduce the resident prey to a density $<10^{-5}$ times the preinvasion density are classified as producing extinction. We chose this threshold because many natural population sizes are $<10^8$; for this size, our threshold implies a minimum $<1,000$ for such a population, and frequent drops

to such a size at least greatly increase the probability of extinction (Lande et al. 2003). We also assume that if the invader drops six orders of magnitude below its initial maximum density, it also goes extinct (we use a lower threshold here because the transient maximum in species 2 is generally much higher than its eventual equilibrium). Additional trials suggested that our results are insensitive to the initial density of the invader and are relatively insensitive to the extinction threshold. Although precise predictions of extinction probability require a stochastic model with discrete variables, the assumption that low densities in continuous-state variable models imply extinction has a long history (e.g., Rosenzweig 1971; Gilpin 1975). We classify a set of parameters as leading to coexistence if the four-species system can be built up by at least one invasion sequence in which transient dynamics do not cause any of the species to drop below these threshold densities.

The result of applying the above procedure to another example is shown in figure 3. There are two important conclusions from this figure. First, a significant range of death rates of the less vulnerable prey result in “extinction” of either the more vulnerable prey or the predator followed by the less vulnerable prey during the course of the transient dynamics. Second, this range of parameters leading to extinction is larger when the top predator has relatively slow dynamics (low e) and relatively high efficiency (low D/e). Extinction of prey 2 during transient dynamics in a system with prey 2 initially resident is possible for a relatively narrow range of parameters at high s_2 and high d_2 . However, all of these systems can be assembled by invasion of species 2 into a chain with species 1 resident, so they do not alter the coexistence conditions shown in figure 3.

Greater demographic rates of the more vulnerable species also increase the chance that it will drop to very low levels under the combined pressures of high predator densities and competition from a less vulnerable prey. If we reexamine the examples in figure 3 but increase both conversion efficiency (b_1) and per capita death rate (d_1) of the more vulnerable species 10-fold, the coexistence areas are greatly reduced even though mutual invasion conditions are unaffected. If we take the example of an invulnerable second “prey” with $s_2 = 0$ (the left-hand side of the X-axis in fig. 3), the minimum values of d_2 allowing coexistence are increased from 0.62 to 1.475 for the case of $e_i = 0.1$ in figure 3A and from 2.01 to 2.53 in figure 3B. The latter example ($d_{2\min} = 2.53$) means that more than 87% of the range of d_2 that produces initially successful mutual invasion actually results in exclusion of the vulnerable prey. In contrast, proportional changes in the demographic rates of the less vulnerable prey 2 have little effect on the parameter ranges yielding extreme densities in the transient phase of the dynamics following invasion.

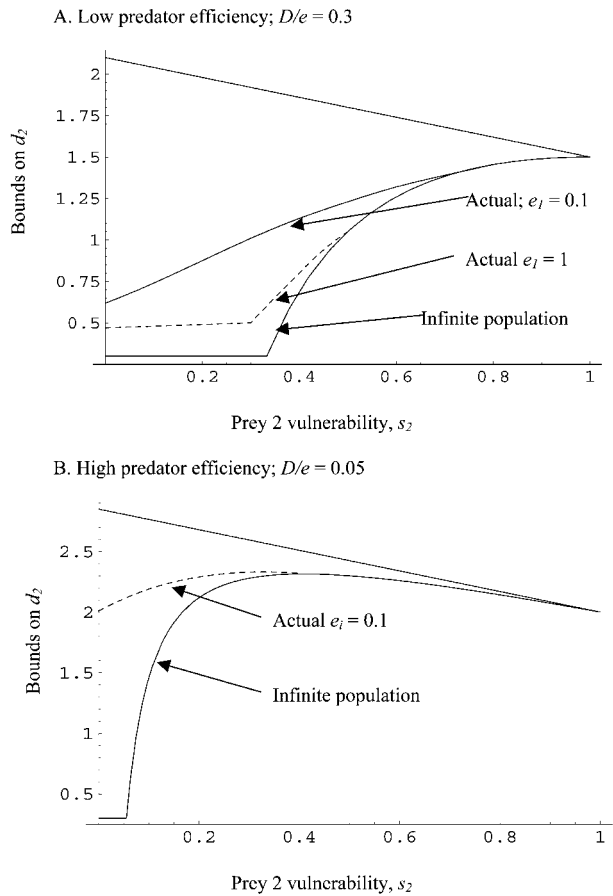


Figure 3: Upper and lower boundaries of d_2 , the per capita death rate of the less vulnerable prey allowing assembly of the full four-species community. The parameters of the system in *A* are $c_1 = c_2 = 1$, $b_1 = 1$, $b_2 = 3$, $r = K = 1$, $s_1 = 1$, $d_1 = 0.1$, $e_1 = e_2$, $D = 0.3e_1$. For the assumed constant predator efficiency ($D/e = 0.3$), the value of e_1 does not affect the equilibrium point or the upper boundary for d_2 . The lower boundary in an arbitrarily large population is also independent of e_1 . However, if the populations are finite, e_1 does affect the lower boundary of d_2 by altering the transient dynamics. The boundaries labeled “actual” indicate the value of d_2 below which at least one species crosses the extinction threshold for a given value of e_1 . The sharp bend in the dashed line occurs because to the left of the bend, extinction of the predator is what prevents coexistence for lower values of d_2 ; to the right of the bend, extinction of prey 1 prevents coexistence. *B* presents the same analysis for a system in which $e_1 = 0.1$ and $D = 0.005$.

More nearly equal competitive abilities of the two prey species also produce a greater crash in the density of species 1 following invasion by species 2. Either increasing c_2 or decreasing d_2 increases the relative competitive strength (and initial per capita growth rate on invasion) of prey 2, allowing it to deplete the resource to a greater extent before the predator dies off and prey 1 recovers. Hence, for a given value of c_2 , decreasing d_2 increases the duration of

the transients as well as their amplitude (meaning a smaller minimum N_1 during the transient). Increasing c_2 for a fixed value of d_2 has a similar effect.

There are two consequences of increasing the vulnerability of the resistant prey, s_2 , above 0. One is that prey 2 is depressed by the predator, lessening resource competition with prey 1. This effect by itself will increase the minimum density of prey 1 during the transient cycles. On the other hand, increasing s_2 also provides sustenance to the predator; this effect alone would reduce the minimum N_1 . The net effect of increasing s_2 may thus be to broaden or to narrow the parameter region yielding extinction of species 1 during the transient dynamics. The fact that the extinction boundary in figure 3 slopes upward as s_2 increases along the X-axis means that the effect of increased predator numbers outweighs the effect of reduced resource competition; increasing s_2 greatly decreases the minimum density of N_1 in the initial transient. In figure 3A, for example, if $d_2 = 0.5$ and $e_1 = 0.1$, the minimum N_1 relative to the equilibrium is approximately 9.01×10^{-7} when $s_2 = 0$, 9.16×10^{-13} when $s_2 = 0.1$, 6.78×10^{-13} when $s_2 = 0.2$, and 6.66×10^{-27} when $s_2 = 0.3$. However, figure 4 provides a second example where the positive effect of reduced resource competition predominates when s_2 is increased.

The conversion efficiency of the less vulnerable prey into predators, e_2 , affects the ability of the predator to maintain itself when the vulnerable prey is scarce and therefore affects the transients in a manner similar to vulnerability, s_2 . When the less vulnerable prey has a conversion efficiency one-third of that of the more vulnerable prey ($e_1 = 0.1$; $e_2 = 0.033$) and $s_2 = 0.3$, the minimum d_2 (based on 10^{-5}) shown in figure 3A is reduced from 1.01

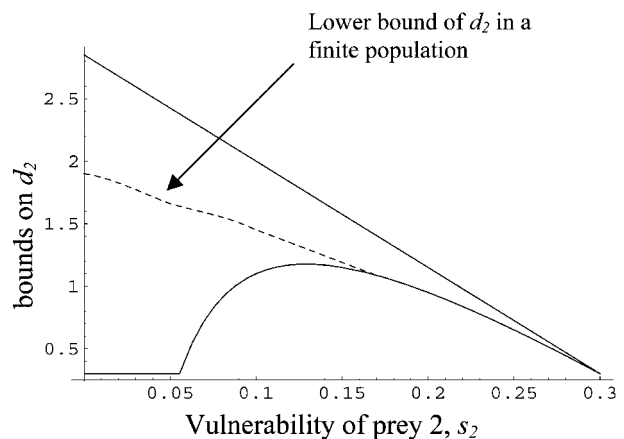


Figure 4: Coexistence boundaries as in figure 3 for an example of equation (1) in which the parameters are $c_1 = c_2 = 1$, $r = K = 1$, $b_1 = 10$, $d_1 = 1$, $b_2 = 3$, $e_1 = e_2 = 1$, $s_1 = 1$, $D = 0.05$.

to 0.68, making coexistence occur over a broader range of species properties. Conversely, coexistence conditions become more restrictive when e_2 is $>e_1$.

Increasing resource productivity via a larger value of K alters coexistence boundaries even when transient dynamics have little impact. However, the minimum density of prey 1 during transient cycles (relative to its equilibrium in the three-species food chain) decreases extremely rapidly with resource carrying capacity. For example, if the carrying capacity is doubled in the example shown in figure 2, the minimum transient density of species 2 is reduced by approximately 15 orders of magnitude even though the equilibrium density is reduced by only 20%. Results in appendix B in the online edition of the *American Naturalist* show that a proportional increase in K is equivalent to proportional increases in the conversion efficiencies of the two prey, b_i .

The above results are changed quantitatively, but not qualitatively, by changing the exact value of the population threshold used to classify a low density as extinction. For some populations, the five-order-of-magnitude reduction may still be too high a density to result in extinction. However, decreasing the critical density that defines extinction by two or three additional orders of magnitude had relatively modest effects on the parameter ranges allowing coexistence in most of the models we examined. Applying a threshold proportional reduction of 10^{-8} rather than 10^{-5} to figure 3A (with $e_i = 0.1$) reduces the minimum d_2 from 0.62 to 0.335 at $s_2 = 0$ and from 1.01 to 0.855 at $s_2 = 0.3$. These still represent significant reductions in the parameter range predicted to allow coexistence by a simple invasion analysis. Even thresholds of 10^{-20} can significantly change coexistence boundaries in some cases. The length of the transient oscillations is not closely related to the minimum population densities during the initial phases of those oscillations. If we considered the amount of time spent at low densities over the entire course of the transients, the results reported above would also change in a quantitative, but not a qualitative, way.

The above results do not constitute a complete analysis of parameter space for equation (1). However, in appendix B, we scale the model to show that the dynamics depend on only eight parameter combinations. The above calculations describe the effects of changes in all of the parameters of the scaled version of the model presented in appendix B. The efficiency and demographic rates of the predator as well as the demographic rates of the more vulnerable prey seem to be the key parameters determining the relative size of the parameter space where extinction during transient dynamics is likely.

It is important to note that transient fluctuations can affect community assembly at stages before the addition of the less defended prey, which is the last species added

in the assembly process considered here. The addition of a top-level consumer to a food chain can cause large-amplitude transient cycles when the top consumer has a low-equilibrium prey requirement relative to the preadoption equilibrium prey density and when the introduced consumer has dynamics that are rapid relative to its prey (Renshaw 1991; P. A. Abrams and E. G. Noonburg, unpublished results). However, more rapid dynamics of the top consumer are biologically unlikely (Moloney and Field 1989; Cohen et al. 2003) and are the opposite of the conditions that lead to large transients in the final stage of assembly of the diamond web considered here.

It is also important to note that a four-species community could arise by invasion when parameter values do not produce large transients, followed by environmental or evolutionary change in the parameters. However, such a case would still be vulnerable to extinction via transients if the resistant prey were reduced to low levels by appropriate environmental stochasticity.

Alternative Models

In this section, we analyze three alternative models in some detail and briefly consider a variety of other models.

Abiotic (Chemostat) Resources

We consider a modification of the basic model in which the resource enters the environment at a fixed rate ρ ; what is not consumed leaves at per capita rate q . Only the equation for the dynamics of the resource differs from equation (1):

$$\frac{dR}{dt} = \rho - qR - c_1 N_1 R - c_2 N_2 R. \quad (6)$$

This sort of dynamics could represent any resource that enters a system at a rate independent of its density inside the system but leaves at a rate proportional to its current density. Holt et al. (1994), Leibold (1996), and Grover and Holt (1998) use this model of resource growth in their analyses of the diamond web. The three-species equilibrium resource density is

$$R^{*(i)} = \frac{\rho}{q + c_i N_i^{*(i)}}. \quad (7)$$

Equilibria for N_i and P are identical to values derived from the basic model (table 1). The coexistence boundaries can be found from equations (2)–(5) by substituting equation (7) for $R^{*(i)}$.

To make the example comparable to our primary model, we choose ρ so that the maximum growth rate of the

resource is the same as for equation (1) in the system shown in figure 3A ($\rho = 1/4$), and we adjust q so that $R^{*(1)}$, $N_1^{*(1)}$, and $P^{*(1)}$ are identical to the equilibrium densities in that figure. The results (fig. 5) show that transient dynamics still reduce the range of parameters allowing coexistence, although they produce a significantly smaller reduction than in the comparable logistic resource model (fig. 3A) for the case of rapid predator dynamics ($e_i = 1$). It is likely that the constant influx of resources at low resource abundances in the chemostat model shields the prey from very low densities and dampens the transient cycles. However, transient cycles are still sufficiently large to affect coexistence for a significant range of parameters, particularly when predator dynamics are slow ($e_i = 0.1$). As in the case of logistic resource growth, more rapid dynamics of the vulnerable consumer species also shrinks the range of relative prey efficiencies allowing coexistence.

Lotka-Volterra Competition

The second alternative we examine is a model in which the single resource is not represented explicitly but is modeled using the standard Lotka-Volterra competition equations. In this case, the equation for prey 1 is

$$\frac{dN_1}{dt} = N_1[\gamma_1 - k_1(N_1 + \alpha_{12}N_2)] - s_1N_1P \quad (8)$$

where α_{12} is the competition coefficient of prey species 2 on species 1. In the absence of predators and competitors, species 1 has logistic growth with carrying capacity γ_1/k_1 and maximum per capita growth rate γ_1 . The equation for prey 2 is equivalent, with α_{21} being the competition coefficient of species 1 on 2. The predator equation is identical to the basic model (eq. [1]). The Lotka-Volterra competition model does not have the time lags in the effects of resource competition that are present in equation (1) and is more appropriate for direct interference competition or competition for space.

The procedure for finding coexistence boundaries based on mutual invasion conditions is similar to the basic model. Here, we present the invasion conditions in terms of the range of intrinsic growth rates, γ_2 , that allow mutual invasion for all possible vulnerabilities, s_2 , of the weaker resource competitor. For each value of s_2 , the upper limit of γ_2 is set by the condition for prey 1 to invade a system consisting of N_2 and P at equilibrium:

$$\gamma_2 < \frac{s_2\gamma_1}{s_1} - \frac{k_1\alpha_{12}D}{e_2s_1} + \frac{k_2D}{e_2s_2}. \quad (9)$$

Similarly, the minimum γ_2 is set by the invasion condition for prey 2:

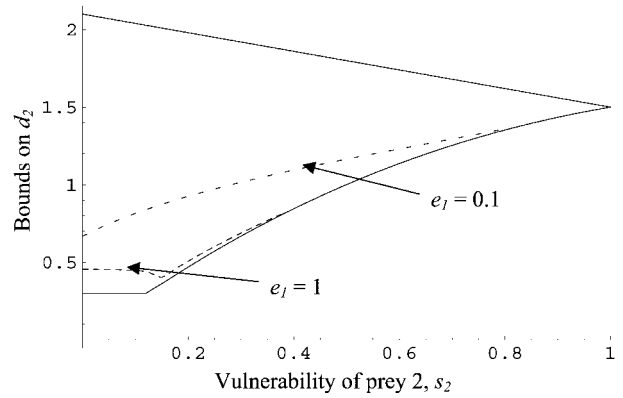


Figure 5: Coexistence boundaries as in figure 3 for a model with chemostat resource dynamics using parameters comparable to figure 3A: $c_i = 1$, $b_1 = 1$, $b_2 = 3$, $r = K = 1$, $d_1 = 0.1$, $e_1 = e_2$, $D/e_i = 0.3$, $s_1 = 1$, $\rho = 0.25$, and $q = (\rho r / \{K[r - (c_i D/e_i s_i)]\}) - (c_i D/e_i s_i)$. The effects of transients on the lower boundary are shown for the cases of $e_i = 0.1$ and $e_i = 1.0$.

$$\gamma_2 > \frac{k_2\alpha_{21}D}{s_1e_1} + \frac{s_2}{s_1} \left(\gamma_1 - \frac{k_1D}{e_1s_1} \right). \quad (10)$$

For $s_2 < k_1\alpha_{12}D/(e_2\gamma_1)$, the predator cannot persist on N_2 , and the maximum γ_2 is set by the invasion condition for prey 1 in the absence of predators:

$$\gamma_2 < \frac{k_2\gamma_1}{k_1\alpha_{12}}. \quad (11)$$

Inequalities (9)–(11) define minimum and maximum values of γ_2 in the absence of transients. The parameters in equation (8) that are comparable to those in equation (1) may be found by setting the intrinsic growth rate γ_i equal to $b_i c_i K - d_p$, the density-dependence parameter k_i equal to $b_i c_i^2 K/r$, and the competition coefficients $\alpha_{ij} = c_j/c_i$. The transients produced by this Lotka-Volterra analogue of the full diamond model are generally similar but have slightly lower amplitudes of fluctuations in the prey species. For example, in figure 3A with $e_i = 0.1$ and $s_2 = 0$, the potential range of d_2 allowing coexistence is reduced by 0.32 by considering transient dynamics. In the comparable version of equation (8), the range of γ_2 allowing coexistence is reduced by 0.30. If s_2 is increased to 0.3 in this example, the range of d_2 allowing coexistence from figure 3A is reduced by 0.71 by transients, while the range of γ_2 is reduced by 0.69, a nearly identical quantitative change. These and other numerical results for the comparable Lotka-Volterra model suggest that the added lag produced by resource dynamics has little impact on

the transient dynamics observed at the two top trophic levels.

Two Resources

It is unlikely that two consumer species will have absolutely identical resource utilization given the stringent criteria needed for a set of entities to qualify as a single homogeneous resource (Abrams 1988). Thus, it is also important to consider how the results are altered when there are two resources that are utilized differently by the two prey. Here, we treat a relatively simple situation with two resources in which each prey has a different “preferred” resource that it captures at a greater rate than its “nonpreferred” resource. The attack rates of prey species 1 on resources 1 and 2, respectively, are κc_1 and $(1 - \kappa)c_1$, while prey 2 has attack rates $(1 - \kappa)c_2$ and κc_2 on resources 1 and 2; κ varies from 0.5 to 1 and describes the degree of specialization on the preferred resource. Thus, resource 1 changes according to

$$\frac{dR_1}{dt} = rR_1 \left(1 - \frac{R_1}{K} \right) - \kappa c_1 R_1 N_1 - (1 - \kappa) c_2 R_1 N_2. \quad (12)$$

The numerical response of each prey species is proportional to its total consumption of both resources, and for simplicity, we assume that the conversion efficiencies of prey i are equal for both resources. This model changes both the theoretical invasion limits and how the transients affect these limits. Although resource partitioning reduces transients, simulations of a range of systems suggest that transients still produce extinction over a wide range of parameters predicted to allow mutual invasion, provided overlap in resource use is substantial. Figure 6 presents results for a two-resource system analogous to that for figure 4. For a wide range of levels of resource overlap (κ), the minimum density of N_1 during transients was still low enough to imply extinction under most reasonable equilibrium population sizes. When κ is significantly above 0.5, the two prey can coexist in the absence of the predator, and a second assembly route (adding the predator as the final species) becomes possible. This modifies the coexistence bounds in a complicated manner. The more vulnerable prey (species 1) still has a low minimum density during the transient dynamics following predator invasion, but this minimum is often not monotonically related to the death rate of prey 2. In the example in figure 6, this invasion sequence becomes possible when $\kappa > 0.6147$, and this makes assembly possible for some intermediate values of d_2 . However, these cases do not represent predator-mediated coexistence and are not germane to the present discussion. Nevertheless, it is important to note that tran-

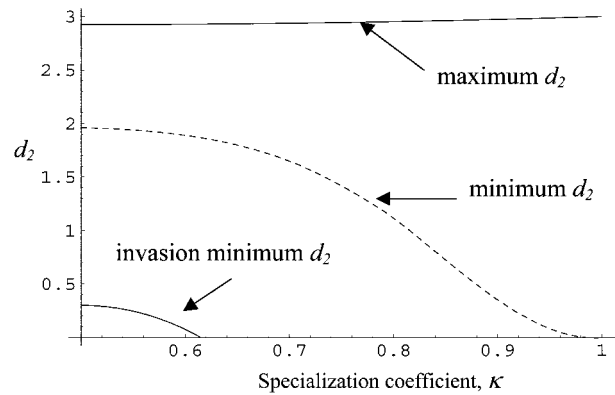


Figure 6: Range of d_2 allowing coexistence of two prey in the two-resource model. The specialization coefficient κ determines resource use of both prey species; $\kappa = 0.5$ implies that both are identical generalists, while $\kappa = 1$ implies that each utilizes a different resource exclusively. The dashed line is the lower limit of d_2 assuming that a five-order-of-magnitude drop implies extinction of a population. The parameter values are $K_i = 1$, $r_i = 1$, $c_i = 1$, $b_1 = 10$, $d_1 = 1$, $b_2 = 3$, $s_1 = 1$, $s_2 = 0$, $e_i = 1$, $D = 0.05$; these are identical to those used in the one-resource model in figure 4.

sient dynamics can lead to exclusion in the presence of the predator, even in cases where coexistence without the predator occurs.

Additional Variations on Equation (1)

There are several related food web models that deserve at least a brief mention here. The following comments are based on more limited simulations of these variant models. First, it is possible to have higher-trophic-level predators that consume the predator species in equation (1). Unless these higher-level predators have alternative foods or direct density dependence, they will eliminate coexistence of prey 1 and 2 by regulating the density of the predator at a fixed abundance. Alternate foods or direct density dependence of these top predators can allow prey coexistence, and at least direct density dependence has a stabilizing impact on the entire system. However, this stabilization often does not sufficiently dampen the crash in prey 1's density following the addition of prey 2 to allow coexistence. Furthermore, including a fifth, as well as a fourth, trophic level reduces the impact of the fourth level on prey dynamics.

A second class of modification of equation (1) is a change to nonlinear functional responses for the consumer species. Most measured functional responses saturate at high prey densities, suggesting that the addition of a handling time to the linear functional responses in equation (1) would produce a more realistic model. Abrams (1999)

showed that sustained limit cycles, which frequently occur in such models, greatly reduced the possibility of coexistence even without a consideration of transient dynamics. However, numerical analysis of these models (P. A. Abrams, unpublished data) shows that the initial (transient) cycles in such cases are much larger in amplitude than are the final cycles, and a consideration of transients produces a reduction in coexistence bandwidth comparable to the models with zero handling time.

A third class of extensions involves the addition of adaptively variable predator defense in the more vulnerable prey species. There is a growing body of theoretical and empirical work showing that adaptive behavior affects community dynamics (reviewed in Bolker et al. 2003). Recent work by Vos et al. (2004) has suggested that inducible defenses can greatly dampen transient fluctuations that would otherwise occur in two- and three-species food chains. We have analyzed a model in which the more vulnerable prey can adaptively adjust its level of defense at the expense of a lower capture rate of the resource. Specifically, we assume that the resource capture parameter c_1 increases with vulnerability s_1 according to a Michaelis-Menten relationship. This means that the vulnerable prey species can become completely defended, but this reduces its resource capture to 0. (Prey 2 is assumed to have no adaptive change in defense because it experiences very little predation in the original model.) Following Abrams and Matsuda (2004), we assumed that the parameter s_1 changes at a rate proportional to the rate at which individual fitness (here, per capita growth rate) increases with the parameter s_1 . This model does increase the transient minimum density experienced by this prey relative to the minimum for equation (1). However, it is necessary that adaptation occur very rapidly to increase the minimum significantly. If there is a minimum predator vulnerability, $s_{1\min}$, that is independent of behavior, the transient minimum density of species 1 (following introduction of prey 2) becomes even less sensitive to behavioral change.

A final possible extension of equation (1) is the addition of a second predator species. However, unless at least one of the predators is limited by some factor other than its food, then two predators cannot persist in a system with only the first prey species. Invasion of the second prey would be required to support a second predator. This leaves us with the same required invasion sequence as in equation (1) with the attendant problem of low population densities during the transient dynamics.

Steiner and Leibold (2004) assembled Lotka-Volterra food webs using randomly generated parameters and compared their dynamics at different productivities. These communities frequently exhibited compositional cycling in which food chains would build up quickly, collapse due to the invasion of a resistant form on a middle trophic

level, and then return to the original food chain. These models have more species than any of those considered here and do not consider transient fluctuations. However, their cyclic long-term dynamics are similar to what is predicted to occur with four species governed by equation (1) when there is repeated reintroduction of species. Transients following introduction of resistant prey cause extinction of the vulnerable prey and the predator. Subsequent reinvasion of the vulnerable prey will displace the resistant prey, the predator will then invade, and the cycle will repeat itself. In another multispecies analysis, Chen and Cohen (2001) studied Lotka-Volterra food web models with up to 30 species. Although they did not report minimum densities, they found that the maximum amplitude of the transient fluctuations that followed a perturbation increased as the number of species in the web increased.

Summary of the Results of Variant Models

The conclusion from the various modifications of equation (1) considered here is that the transient oscillations that significantly restrict the opportunity for coexistence of species based on equation (1) are found in a wide range of related food webs involving both shared predation and shared resources. The models considered here assume a temporally constant and spatially homogeneous environment, which is true of most previous analyses of keystone predation (e.g., Armstrong 1979; Abrams 1993, 1999, 2004; Holt et al. 1994; Leibold 1996). Temporal environmental stochasticity is likely to increase the probability of extinction during transient oscillations (Lande et al. 2003). Spatial structure of the environment may permit coexistence via cyclic colonization-extinction dynamics in each patch as in the repeated reintroduction scenario described in the preceding paragraph.

Discussion

Review of Findings and Predictions

The result that we have stressed above is that the conditions for coexistence of species sharing a resource and a predator are likely to be much more stringent than has previously been thought (e.g., Chase and Leibold 2003). In a food web that is assembled by successive invasions of species, the transient dynamics that occur after an invasion can force one or more resident species to a density that is low enough that extinction is virtually assured. Our analysis suggests that such transients are likely to occur when the less vulnerable competitor invades a system containing both the predator and the more vulnerable prey. Hence, the system does not reach a final state with both competitors present despite having a stable four-species

equilibrium. This phenomenon substantially reduces the region of parameter space in which predator-mediated coexistence is predicted by a standard equilibrium analysis. In many cases, the region is reduced by more than one-half, so this is far from a trivial effect. We have noted above that the reduction can be as much as 90% in some situations where the “less vulnerable” prey species is actually completely invulnerable to the predator. This casts some doubt on a number of recent analyses arguing that the diamond-shaped web contributes strongly to multi-species coexistence in biological communities (Leibold 1996; Grover 1997; Chase and Leibold 2003). These theoretical studies and others have used an equilibrium-based analysis that does not take into account the transient dynamics that follow invasion. Our findings imply that even when the better competitors among the prey species are more vulnerable to predators, the effects of predators on prey biodiversity may not be positive. There has been a surprising lack of consistency in the results of empirical studies that have attempted to determine how predators alter the number of prey species that can coexist; different systems suggest that predators increase or decrease the diversity of competing prey (reviewed in Chase et al. 2002). The work presented here is certainly one factor that will influence the answer to this question. Most of our models have focused on the special case where two prey species are completely unable to coexist without the predator. However, we showed that transient dynamics can also produce exclusion in systems with two or more resources and resource partitioning between the prey species. In these latter cases, the coexistence without the predator may be possible in some cases where it is either impossible or less likely in the presence of the predator because of transient fluctuations. Again, the results presented here predict that positive effects of a generalist predator on the number of coexisting prey will be most likely when the predator has relatively rapid dynamics, when the predator is not very efficient, and when the competing prey consume abiotic (*sensu* Armstrong and McGehee 1980) rather than biotic resources. It would be interesting to determine whether there was a correlation between any of these factors and the observation that predator addition increased the number of coexisting prey species.

Empirical Evidence for Transient Dynamics

One of the most thoroughly studied empirical examples of the diamond web is a laboratory system in which two strains of *E. coli* are the prey and a bacteriophage is the predator (Bohannon and Lenski 1999, 2000). Bohannon and Lenski's (1999) initial experiment began with a system having both more and less vulnerable strains of *E. coli* but was invaded by an invulnerable strain. The invasion of

this form did not appear to produce any extreme oscillations in density. However, this is to be expected in a system where the predator has much more rapid dynamics than does the prey (Bohannon and Lenski [1999] estimate that, on average, 98 phage are produced for each infected bacterium) and where the lowest trophic level (glucose) has chemostat dynamics.

Other than this microbial system, we have been unable to find examples of laboratory or field studies in which the dynamics of both prey were followed after introducing a resistant competitor into a three-species food chain. However, there are indications from both field and lab studies that coexistence can be affected by transient dynamics in larger food webs. Warren et al. (2003) assembled communities in the laboratory using six species of protists. They found that a number of communities that would persist when all species were introduced at sufficiently high densities could not be produced by sequential introductions of rare invaders. They also found that “the time required to reach a persistent state after invasions is long enough, in some cases, to require investigation of assembly along the transients of the resident population densities” (Warren et al. 2003, p. 1,010). Fox (2004) also suggested that there were likely to be long-lasting transients in his experimentally assembled communities consisting of several species of phytoplankton and herbivores. In a comparison of short- (3-year) and long- (≥ 20 -year) duration field experiments involving nutrient addition to lakes, Dodson et al. (2000, p. 2,662) concluded, “Experimental addition of nutrients produced varied and unpredictable responses in species richness, probably due to transient dynamics and time lags.” We could not determine whether these results were driven by diamond-shaped subwebs within these systems, but aquatic communities are some of the systems in which such subwebs are most often described.

Empirical Evidence for Parameter Values in Diamond Webs

Conditions that favor high amplitude transient cycles seem likely to occur in a variety of natural communities. In particular, predators often have slower dynamics than their prey as the result of generally larger body size (Moloney and Field 1989; Cohen et al. 2003), and less defended prey species are likely to have more rapid dynamics than their more defended competitors (due to the added developmental time required to produce defensive structures). The aquatic systems that are frequently the subject of such analyses typically fit these conditions. For example, Andersen's (1997) book includes a review of measured maximum per capita growth rate of zooplankton grazers and the phytoplankton prey. The zooplankton intrinsic growth rates range from 0.12 to 0.82 (d^{-1}), with a median of 0.36

(d^{-1}); the phytoplankton intrinsic growth rates range from 0.23 to 3.40 (d^{-1}), with a median of 1.22 (d^{-1}). This suggests that predator dynamics are generally significantly slower than prey dynamics in nutrient-phytoplankton-zooplankton systems. Another factor that is important in generating transient dynamics is a low food intake requirement of the predator. Andersen's (1997) review of measured threshold food levels for different zooplankton species found that the minimum and maximum values differed by approximately a factor of 50. This suggests that there should be many zooplankton predators whose efficiency is high enough to generate long transients. For comparison, the food requirement for the predator in the system illustrated in figure 2 (where there are large transient cycles) is only one-sixth of the maximum requirement that will allow predators to persist on the better prey species. In applying our results to planktonic systems, however, it is important to note that their population sizes are often large enough to withstand high-amplitude transients and that egg banks or resting stages could provide a stabilizing mechanism in such systems. More generally, work on predator-prey systems suggests that predators most often have growth rates that are significantly less than those of their prey (Moloney and Field 1989) and that predators produce a reduction in prey densities by at least a factor of two (Sih et al. 1985), suggesting a relatively high efficiency.

Our work suggests several potential explanations for observed coexistence in systems in which prey share predators and resources. These include resource partitioning between prey species, spatial heterogeneity, the presence of abiotic resources, or simply very large population sizes. All of these potentially apply to many nutrient-algal-grazer systems. Even if local coexistence cannot occur, regional coexistence in an array of similar habitat patches with immigration may be possible. Here, regional coexistence may involve a shifting pattern of invasion and exclusion, with the more vulnerable prey species arriving in a resource-only patch, the predator invading next, both these species being excluded by the invulnerable prey, and that prey in turn being excluded by new immigrants of the more vulnerable prey, which is a better competitor.

The results outlined here could apply to coexistence of genotypes as well as species. It is clear that large transient oscillations are also expected when a well-defended mutant type arises in a vulnerable prey population under asexual reproduction. Dominant mutants of large effect in sexual populations are also likely to produce large transients under similar conditions. Although evolutionary change in interactions is not included in equation (1), the preliminary results for the model with adaptively changing defense in the more vulnerable species suggests that transient oscillations may still be an important cause of extinctions when there is adaptive change in prey defense.

Implications beyond the Diamond Food Web

For the vast majority of theoretical studies of food web dynamics, there is no evidence that the investigator examined the amplitude of the transient cycles that follow invasion of one or more components of the community. The two authors of this study have certainly been guilty of this failing in the past. Yet it is clear from our analysis of slightly more complicated models that the diamond food web is not the only type of system in which transient fluctuations may effectively prevent coexistence of a set of species. Such transients could have a major impact on the types of communities that are likely to persist in a stochastic environment. A wide range of models in ecology and evolution have assumed coexistence when all component species or types can invade and when successful invasion is eventually followed by dynamics that are bounded away from zero (e.g., all of the models in books by MacArthur [1972], Tilman [1982], and Chase and Leibold [2003], to name a few). We need to understand when coexistence really follows from these conditions if we are to predict what environmental changes might either allow or eliminate coexistence.

Previous discussion of transients in models has focused on the possibility that coexistence might be maintained for relatively long periods in systems where exclusion was the ultimate outcome (McCann and Yodzis 1994; Hastings 2004). This work shows that the opposite phenomenon also occurs. Holt and Hochberg (2001) were apparently the first to note this possibility for systems with more than two species. They presented a single numerical example of apparent competition where prey coexistence is rendered less likely because of a crash in the abundance of one prey species following introduction of a second prey species. This example is similar to our two-resource model with no overlap in resource use by the two prey; as in that model, Holt and Hochberg's (2001) system does not produce minimum prey densities nearly so small, relative to equilibrium, as in the model of the diamond web discussed here. However, even transients with minima that are only two or three orders of magnitude less than the equilibrium density are likely to be important in small populations. In fact, the possibility of such transients reinforces that argument (Abrams 2002) that current conservation biology should be paying more attention to the community ecological context of the focal species. Exclusion due to transient dynamics is likely to occur in some two-trophic-level systems with competition for biotic resources. A theoretical example is provided by Abrams's (1998) two-consumer/two-resource model. In this case, one consumer, when present alone, will cause extinction (via apparent competition) of the resource that it consumes more rapidly. The first consumer will then be forced to very low

densities by invasion of a competing consumer that is better at exploiting the remaining resource. Whether the first consumer is actually excluded or recovers depends on its absolute initial population size and the amount of time required for regrowth of the depleted resource.

There has been considerable interest in the question of whether biological communities have alternative states (e.g., Scheffer et al. 2001; Scheffer and Carpenter 2003). If the sorts of dynamics that are demonstrated here are common, then what appear to be alternative states may represent the fact that some invasion sequences result in the loss of some potential community members via large amplitude cycles. This possibility has significant management implications if one of the states is deemed more desirable than the other. It is usually very difficult to shift one of two or more true alternative attracting states to another configuration. However, it is possible that some of the presumed alternative states are simply the by-product of species loss during large transient cycles. If this is the case, it may be relatively easy to shift the system away from a particular state by a low level of immigration of some or all species.

The transient cycles that we describe for this deterministic model are likely to result in sustained oscillations in natural systems where environmental perturbations are likely to keep a system from approaching its equilibrium. Even if species persist during the oscillations, the fluctuations in density have a variety of implications for any larger food web in which such a diamond-shaped module is embedded. For example, if there is nonlinearity in the functional or numerical responses of species on a fourth trophic level, oscillations of the third level decrease the mean population growth of that fourth-level species and may exclude it entirely (Abrams and Roth 1994). There are no doubt many more food webs in which high-amplitude transient cycles can make a difference between existence and extinction.

The four-species food web given by equation (1) is clearly much simpler than most natural webs. However, many aquatic ecologists have used this model (or a slight variant of it) to represent interactions in natural food webs (Porter 1977; Leibold 1989, 1996; Carpenter 1992; Grover and Holt 1998; Chase and Leibold 2003). Furthermore, the central result is preserved under many modifications of the model, including different resource growth functions, different functional responses, and the presence of more than one resource with resource partitioning between prey species. Our preliminary results suggest that similar transient cycles occur in many larger food webs in which a diamond-shaped model is embedded. Certainly, the widespread lack of explicit analysis of transients suggests that many previous models predicting coexistence of either species or genotypes should be reexamined in light

of the possibility that transient cycles during assembly of the community may prevent coexistence.

Acknowledgments

E.G.N. was supported by a postdoctoral grant from the Great Lakes Fisheries Commission. P.A.A. was supported by a grant from the Natural Sciences and Engineering Research Council of Canada and a fellowship from the J. S. Guggenheim Foundation. We thank R. Law and an anonymous reviewer for comments on an earlier draft of the article.

Literature Cited

- Abrams, P. A. 1988. How should resources be counted? *Theoretical Population Biology* 33:226–242.
- . 1993. Effect of increased productivity on the abundance of trophic levels. *American Naturalist* 141:351–371.
- . 1998. High competition with low similarity and low competition with high similarity: the interaction of exploitative and apparent competition in consumer-resource systems. *American Naturalist* 152:114–128.
- . 1999. Is predator-mediated coexistence possible in unstable systems? *Ecology* 80:608–621.
- . 2002. Will small population sizes warn us of impending extinctions? *American Naturalist* 160:293–305.
- . 2004. Trait-initiated indirect effects in simple food webs: consequences of changes in consumption-related traits. *Ecology* 85:1029–1038.
- Abrams, P. A., and H. Matsuda. 2004. Consequences of behavioral dynamics for the population dynamics of predator-prey systems with switching. *Population Ecology* 46:13–25.
- Abrams, P. A., and J. Roth. 1994. The effects of enrichment on three-species food chains with nonlinear functional responses. *Ecology* 75:1118–1130.
- Andersen, T. 1997. *Pelagic nutrient cycles*. Springer, New York.
- Armstrong, R. A. 1979. Prey species replacement along a gradient of nutrient enrichment: a graphical approach. *Ecology* 60:76–84.
- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* 115:151–170.
- Bohannan, B. J. M., and R. E. Lenski. 1999. Effect of prey heterogeneity on the response of a model food chain to resource enrichment. *American Naturalist* 153:73–82.
- . 2000. The relative importance of competition and predation varies with productivity in a model community. *American Naturalist* 156:329–340.
- Bolker, B. M., M. Holyoak, V. Krivan, L. Rowe, and O. Schmitz. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology* 84:1101–1114.
- Carpenter, S. R. 1992. Destabilization of planktonic ecosystems and blooms of blue-green algae. Pages 460–481 in J. F. Kitchell, ed. *Food web management: a case study of Lake Mendota*. Springer, New York.
- Case, T. J., and R. G. Casten. 1979. Global stability and multiple domains of attraction in ecological systems. *American Naturalist* 113:705–714.
- Chase, J. M. 1999. Food web effects of prey size refugia: variable

- interactions and alternative stable equilibria. *American Naturalist* 154:559–570.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The effects of predators on competition between their prey. *Ecology Letters* 5:302–313.
- Chen, X., and J. E. Cohen. 2001. Transient dynamics and food-web complexity in the Lotka-Volterra cascade model. *Proceedings of the Royal Society of London B* 268:869–877.
- Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the USA* 100:1791–1796.
- Cramer, N. F., and R. M. May. 1972. Interspecific competition, predation, and species diversity: a comment. *Journal of Theoretical Biology* 34:289–293.
- Dodson, S. I., S. E. Arnott, and K. L. Cottingham. 2000. The relationship in lake communities between primary productivity and species richness. *Ecology* 81:2662–2679.
- Fox, J. W. 2004. Effects of algal and herbivore diversity on the partitioning of biomass within and among trophic levels. *Ecology* 85:549–559.
- Gilpin, M. E. 1975. *Group selection in predator-prey communities*. Princeton University Press, Princeton, NJ.
- Goh, B. S. 1977. Global stability in many-species systems. *American Naturalist* 111:135–143.
- Grover, J. P. 1997. *Resource competition*. Chapman & Hall, New York.
- Grover, J. P., and R. D. Holt. 1998. Disentangling resource and apparent competition: realistic models for plant-herbivore communities. *Journal of Theoretical Biology* 191:353–376.
- Hastings, A. 2001. Transient dynamics and the persistence of ecological systems. *Ecology Letters* 4:215–220.
- . 2004. Transients: the key to long-term ecological understanding? *Trends in Ecology & Evolution* 19:39–45.
- Hastings, A., and K. Higgins. 1994. Persistence of transients in spatially structured ecological models. *Science* 263:1133–1136.
- Holt, R. D., and M. E. Hochberg. 2001. Indirect interactions, community modules and biological control: a theoretical perspective. Pages 13–37 in E. Wajnberg, J. K. Scott, and P. C. Quimby, eds. *Evaluating indirect ecological effects of biological control*. CABI International, New York.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* 144:741–771.
- Lande, R., S. Engen, and B.-E. Sæther. 2003. *Stochastic population models in ecology and conservation: an introduction*. Oxford University Press, Oxford.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134:922–949.
- . 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. *American Naturalist* 147:784–812.
- Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28:467–494.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper & Row, New York.
- McCann, K., and P. Yodzis. 1994. Nonlinear dynamics and population disappearances. *American Naturalist* 144:873–879.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarette, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249–286.
- Mills, O. S., M. E. Soule, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219–224.
- Milo, R., S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii, and U. Alon. 2002. Network motifs: simple building blocks of complex networks. *Science* 298:824–827.
- Moloney, C. L., and J. G. Field. 1989. General allometric equations for rates of nutrient uptake, ingestion, and respiration in plankton organisms. *Limnology and Oceanography* 34:1290–1299.
- Noonburg, E. K., B. J. Shuter, and P. A. Abrams. 2003. Indirect effects of zebra mussels on the planktonic food web. *Canadian Journal of Fisheries and Aquatic Science* 60:1352–1368.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Phillips, O. M. 1974. The equilibrium and stability of simple marine systems. II. Herbivores. *Archiv für Hydrobiologie* 73:310–333.
- Porter, K. G. 1977. The plant-animal interface in freshwater ecosystems. *American Scientist* 65:159–170.
- Renshaw, E. 1991. *Modelling biological populations in space and time*. Cambridge University Press, Cambridge.
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18:648–656.
- Scheffer, M., S. R. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16:269–311.
- Steiner, C. F., and M. A. Leibold. 2004. Cyclic assembly trajectories and scale-dependent productivity-diversity relationships. *Ecology* 85:107–113.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- Vance, R. R. 1974. Predation and resource partitioning in one-predator-two-prey model communities. *American Naturalist* 112:797–813.
- Volterra, V. 1931. Variations and fluctuations of the number of individuals in animal species living together. Pages 409–448 in R. N. Chapman, ed. *Animal ecology*. McGraw Hill, New York.
- Vos, M., B. W. Kooi, D. L. DeAngelis, and W. M. Mooij. 2004. Inducible defences and the paradox of enrichment. *Oikos* 105:471–480.
- Warren, P. H., R. Law, and A. J. Weatherby. 2003. Mapping the assembly of protist communities in microcosms. *Ecology* 84:1001–1011.