

# Effects of predation pressure on species packing on a resource gradient: insights from nonlinear dynamics

John Vandermeer<sup>a,b,\*</sup>, Heidi Liere<sup>a</sup>, Brenda Lin<sup>b</sup>

<sup>a</sup>*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA*

<sup>b</sup>*School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109, USA*

Received 18 October 2004

Available online 25 January 2006

## Abstract

The classical case of three competitors arranged on a resource gradient such that the central competitor will be excluded due to competition from the other two is studied from the point of view of the effects of added predators. The basic formulation is motivated by a desire to understand the effects of asymmetries in multidimensional Lotka–Volterra systems. We first study the effects of perfectly specialist predators and find a rich collection of possible behaviors of the system including (1) extinction of all predators and subsequent extinction of the subordinate competitor, (2) dominant competitors and their predators coexist but the subordinate competitor goes extinct, (3) all species except the predator of the subordinate competitor coexist in coordinated phase-reversed chaos, (4) exclusion of one or more species occurs through an expanding heteroclinic cycle, and (5) all species coexist in an uncoordinated chaos. We then study the effects of five qualitatively distinct forms of polyphagy. In one case, corresponding to the well-known vulnerability to predation versus competitive ability trade-off, it is possible to have the subordinate competitor be the only survivor in the system. The other three cases of polyphagy lead to distortions in the basic pattern seen in the previously analyzed specialist case. Studying this case of ecologically motivated asymmetries in the basic Lotka–Volterra formulation is a step in the direction of fully understanding interacting populations. © 2006 Elsevier Inc. All rights reserved.

*Keywords:* Limiting similarity; Competition; Predation; Heteroclinic cycles; Chaos

## 1. Introduction

The original concept of limiting similarity and species packing (MacArthur and Levins, 1967) includes the idea that in a system with three competitors, if the competitors are arranged in a chain where species 1 competes with species 2, species 2 competes with species 3, but species 1 and 3 compete weakly or not at all, if competition against species 2 is too large, the system will be reduced to species 1 and species 3. The situation represents the classic case of three species on a single environmental gradient, in which the amount of overlap of the second with either the first or third is thought to represent the degree of competition of the two “dominant” competitors (species 1 and 3) against

the “subdominant” (species 2). If that competitive effect becomes too strong, the subdominant is eliminated from the system. Levins and MacArthur noted the simple but powerful idea that if species 2 were removed from the system, the niche overlap of species 1 and 3 would be such that another species, perhaps not as susceptible to competition as the former number 2, could invade. Thus, there would be a kind of balancing act in which a suite of species exist on an environmental gradient in such a way that they would be optimally “packed,” and the idea of limiting similarity (equivalent to Gause’s principle) became linked with the idea of species packing. A great deal of subsequent literature has treated this subject, directly or indirectly (e.g., MacArthur, 1970; Abrams, 1983; Pacala and Tilman, 1994; Leibold, 1998; Kinzig et al., 1999; Chesson, 2000).

A related literature has evolved regarding the effect of predators (or parasites, diseases, herbivores) on the process of competition. It is an intuitive idea that one way of

\*Corresponding author. Department of Ecology and Evolutionary Biology, University of Michigan, 830 N. University, Ann Arbor, MI 48109, USA. Fax: +1 734 647 0884.

E-mail address: [jvander@umich.edu](mailto:jvander@umich.edu) (J. Vandermeer).

stabilizing a system of inherently unstable competitors is with predatory pressure. The idea has frequently been taken as almost axiomatic, from observations of Darwin (1998), to an explicit statement by Hutchinson (1948), to the keystone predator effect (Paine, 1974), to extensive experiments with herbivores in grasslands (Harper, 1996; Ryerson and Parmenter, 2001; Bakker and Olf, 2003), to the “Janzen/Connell hypothesis” (Janzen, 1970; Connell, 1971, 1978; Cordiero and Howe, 2003) to more recent work with more complicated food webs (Spiller and Schoener, 1990; Yodzis, 1995; deRoos et al., 1991, 1998; Vandermeer et al., 2002; Vandermeer and Pascual, 2005) and the implied top down effect of predators on a lower trophic level (e.g., Schmitz, 2003). Mathematical theory has been extensively employed to study this effect (Parrish and Sella, 1970; Cramer and May, 1972; Roughgarden and Feldman, 1975; Fujii, 1977; Hsu, 1981; Hutson and Vickers, 1983; Kirlinger, 1986; Hofbauer and Sigmund, 1989; Vandermeer, 1991; Schreiber, 1997, 1998).

These two ideas, species packing and control from above, are strongly embedded in the ecological literature. Yet an analysis of the consequences of putting them together has never been systematically undertaken in the context of the full complexity of non-linear dynamics that emerge from oscillating systems. The important insights of earlier workers, as reflected in the literature cited in the previous paragraph, are mainly consequences of assuming ultimately equilibrium dynamics. By formulating the problem with strong competition against the subdominant competitor, we admit to the possibility of complicated behavior. Whether such complicated behavior actually exists in nature remains an open question and is not the focus of this work. Nevertheless, given the history of these two ideas in the ecological literature, and given our modern understanding of the important role of complex dynamics in species coexistence (e.g., Huisman and Weissing, 1999, 2001a, b; Vandermeer and Pascual, 2005), exploring the behavior of this particular formulation is warranted.

Furthermore, the present investigation can be viewed as an extension of earlier work in which multiple competitors were subjected to the influence of multiple predators in a perfectly symmetrical system (Schreiber, 1997, 1998; Vandermeer and Pascual, 2005). As suggested in that work, the full symmetry of the system was largely artificial and the system was constructed in that fashion specifically for the purpose of developing a baseline understanding of its behavior in a non-equilibrium situation. Relaxing that symmetry was stated as a subject of future research. Yet relaxing the symmetry of a generalized predatory effect on competitors could be done in many different ways. The present analysis is one such way, motivated by the classical structure of three species along a single resource gradient. As will be seen, the underlying importance of heteroclinic cycles (Vandermeer and Pascual, 2005) remains, but with rather dramatic complicating effects of the asymmetry.

Therefore, we consider the case in which a competitor is subdominant due to competition exerted on it by two other

species, referred to here as dominant competitors. We study the specific case in which the subdominant competitor is expected to be eliminated through strong competition from the dominant competitors, and ask first, what pattern of predation pressure on all competitors would lead to a reversal of this expected outcome, and second, what sorts of population behavior patterns would be expected if such an outcome occurred? We concern ourselves with the admittedly restricted case in which strong competition (by which we mean competition coefficients greater than unity) is coupled with symmetry (in both the strong competitive effect and the predatory effects). Effects of relaxing those assumptions do not seem to alter the main conclusions, as noted in the discussion section. We also note here that the parameter values we used to study the system seem not to matter much in the general qualitative results, as long as they are in the zone of producing oscillations in the parent subsystems.

## 2. The basic model

The situation we model is one in which three competitors are arranged on a single environmental gradient, as conceived originally by MacArthur and Levins (1967). We do not explicitly consider the environmental gradient as a state variable, but rather model the system in classic Lotka–Volterra form in which the species are imagined to be arranged on the environmental gradient in the order 1, 2, and 3 and have the consequent dynamic structure that would result from such an arrangement. That is, competitor 1 ( $x_1$ ) competes with competitor 2 ( $x_2$ ) and competitor 2 competes with competitor 3 ( $x_3$ ), but competitor 1 and competitor 3 do not compete with one another. Furthermore, we are interested in the strictly unstable (or bistable) case of competition, that is, where  $x_2$  is not able to withstand the joint competitive pressure from  $x_1$  and  $x_3$ . So, with the classic Lotka–Volterra competition formulation, where  $\alpha_{ij}$  is the competition effect of species  $j$  on species  $i$ , we stipulate  $\alpha_{13}, \alpha_{31} = 0$ , and  $\alpha_{12}, \alpha_{21}, \alpha_{32}, \alpha_{23} = 1.1$ . Assuming the classic Lotka–Volterra form for predation (with a type II, or “diminishing returns” type functional response) we take the following equations as governing the system:

$$\dot{P}_1 = -mP_1 + aP_1[x_1 + \beta_2x_2 + \beta_1x_3]\Theta_1, \quad (1a)$$

$$\dot{P}_2 = -mP_2 + aP_2[x_2 + \beta_2x_1 + \beta_3x_3]\Theta_2, \quad (1b)$$

$$\dot{P}_3 = -mP_3 + aP_3[x_3 + \beta_3x_2 + \beta_1x_1]\Theta_3, \quad (1c)$$

$$\dot{x}_1 = x_1[1 - x_1 - 1.1x_2] - ax_1(P_1\Theta_1 + \beta_2P_2\Theta_2 + \beta_1P_3\Theta_3), \quad (1d)$$

$$\dot{x}_2 = x_2[1 - x_2 - 1.1(x_1 + x_3)] - ax_2(P_2\Theta_2 + \beta_2P_1\Theta_1 + \beta_3P_3\Theta_3), \quad (1e)$$

$$\dot{x}_3 = x_3[1 - x_3 - 1.1x_2] - ax_3(P_3\Theta_3 + \beta_3P_2\Theta_2 + \beta_1P_1\Theta_1), \tag{1f}$$

$$\Theta_1 = \frac{1}{[1 + b(x_1 + \beta_2x_2 + \beta_1x_3)]}, \tag{1g}$$

$$\Theta_2 = \frac{1}{[1 + b(x_2 + \beta_2x_1 + \beta_3x_3)]}, \tag{1h}$$

$$\Theta_3 = \frac{1}{[1 + b(x_3 + \beta_3x_2 + \beta_1x_1)]},$$

where  $x_i$  is the biomass of the  $i$ th competitor,  $P_i$  is the biomass of the  $i$ th predator,  $\beta_j$  is the proportion of competitor  $j$  used by the appropriate predator,  $a$  is the predation rate,  $m$  is the mortality rate of the predator, and  $b$  is the parameter of the functional response. The system is illustrated in Fig. 1. From the set-up of the equations it is obvious that we are considering the symmetrical case with respect to the competition coefficients (both equal to 1.1), the specialized predation pressure (parameter  $a$ ), and the polyphagy coefficients (the  $\beta$ 's). System 1 is well known, at least in lower dimensional forms, to generate oscillations, some of which can be extreme, as discussed in the following sections.

Biologically it makes little sense to consider populations that are below a certain critical value. For biological realism, when running simulations with system 1, we set a lower limit of  $10^{-8}$ , below which the population density is set equal to zero. Nevertheless, to explore the general mathematical behavior that gives rise to the biological results, it is frequently useful and even necessary to eliminate this piece of biological realism. Thus, throughout this paper we sometimes use the lower limit as a cut off point, and sometimes not, the context making it clear whether the biological or mathematical focus is being used.

Note that with either pair of competitors ( $x_1$  and  $x_2$  or  $x_3$  and  $x_2$ ) it would be impossible to identify a competitive dominant since the symmetrical competition coefficient is identical for either member of the pair. However, considering the system as a whole, it is clear that the topology of the food web results in  $x_2$  being subdominant in the sense that it will inevitably be extinguished from the

system in the absence of predation. We thus refer to  $x_2$  as the “subdominant” and  $x_1$  and  $x_3$  as the “dominant” competitors. This terminology may be a bit at variance with some of the literature that defines dominance based on the competitive ability of a particular species as compared to the competitive ability of some other species. However, we feel that the use of dominant versus subdominant in the present case does not violate the spirit of the original idea in that the dominant will survive and the subdominant will be extinguished in the case of predator-free competition.

We begin with the case of perfectly specialized predators, which is to say  $\beta_i = 0$  for all  $i$ . The pattern of coexistence, including the nature of the population dynamics involved, is studied in detail for this case. We then turn to the various cases of polyphagy. There are two cases of symmetrical polyphagy ( $\beta_3, \beta_2 = 0, \beta_1 > 0$ , and  $\beta_3, \beta_2, \beta_1 > 0$ ), and three cases of asymmetrical polyphagy ( $\beta_2 = 0, \beta_3, \beta_1 > 0; \beta_1 = 0, \beta_2, \beta_3 > 0$ ; and  $\beta_1, \beta_2 = 0, \beta_3 > 0$ ). Because of the overall symmetry of the system, the various other topologically possible situations are all equivalent to one or the other of these three cases. All five cases of polyphagy are explored in terms of their biological outcomes.

### 3. The case of specialized predators ( $\beta_i = 0$ )

Simply calculating those values of parameter  $a$  for which  $x_2 > 0$  (using the critical value of  $10^{-8}$ , below which any of the populations is set equal to zero) and  $P_2 > 0$ , we obtain the result illustrated in Fig. 2. Note that when the predation pressure (parameter  $a$ ) reaches a critical point, the competitive exclusion of  $x_2$  is avoided, although its specific predator ( $P_2$ ) continues to be eliminated from the system (obviously the other two predators act to control the dominant competitors). At higher predation pressure  $P_2$  is maintained in the system, along with its food source  $x_2$ . However, in Fig. 2 it is evident that this result is not uniformly true for a critical value of the parameter  $a$ , for in the zone of persistence of either  $P_2$  or  $x_2$ , there are interruptions in which they are indeed driven to extinction. While the general pattern illustrated in Fig. 2 is consistent for any set of initial conditions, the exact positions of the exclusion zones (the white in Fig. 2) change depending on initial conditions, but never extend far to either the left or right for  $x_2$  and never far to the right for  $P_2$ . This is a curious pattern that requires further analysis to fully explain, even though the general biological conclusion is

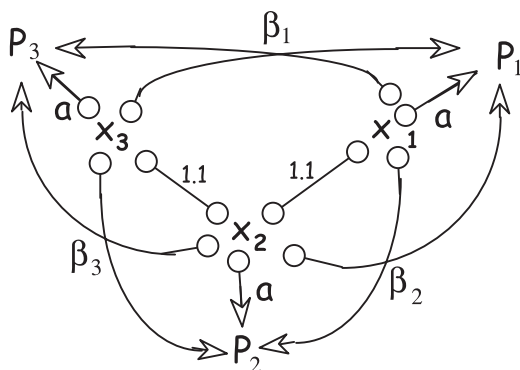


Fig. 1. Diagrammatic representation of system 1 (arrowheads represent positive effect, small circles represent negative effect).

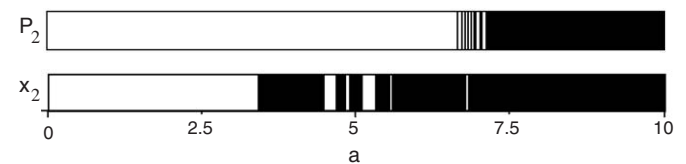


Fig. 2. Qualitative outcome of the dynamics of system 1 for the subdominant competitor ( $x_2$ ) and its predator ( $P_2$ ). Black indicates persistence of the species, white indicates extinction of the species.

clear—that specialist predators can act to eliminate the necessary exclusion of the subdominant competitor.

If the predation rate ( $a$  in Eq. (1)) is too small, the predators cannot be maintained in the system and the resulting competition will remove the interior competitor. This point can be calculated analytically as the minimum predation rate (parameter  $a$ ) for which the predator isocline intersects the prey isocline, which is,

$$m(1 + b) < a.$$

In the case simulated here ( $m = 0.8$  and  $b = 2$ ) the critical value of  $a$  is 2.4. Thus, for any value of parameter  $a$  less than 2.4, we would expect the extinction of all predators and subsequent extinction of  $x_2$  due to competitive pressure from  $x_1$  and  $x_3$ .

As predation rate increases beyond 2.4, subsystems 1 and 3 (i.e.,  $P_1, x_1$ , and  $P_3, x_3$ ) come to exist independently after  $x_2$  is eliminated through competition and subsequently  $P_2$  goes extinct due to an absence of food. As predation rate increases yet further,  $x_2$  is maintained in the system as an anti-phase element in a coordinated chaos between system 1 and 3. This unusual result is illustrated in Fig. 3. The dynamics are intuitively obvious—from the elementary topology of the system, we expect  $x_2$  to be antiphase with both  $x_1$  and  $x_3$  (Vandermeer, 2004), which it is in this chaotic situation (at slightly smaller predation pressure a simple limit cycle with  $x_1$  and  $x_3$  in phase and both out of phase with  $x_2$  also exists). Thus,  $x_2$  apparently drives both  $x_1$  and  $x_3$  to be in phase with one another, even though they are chaotic. Note that in this parameter range, the coordinated chaos occurs in the absence of  $P_2$ , which is

rapidly driven out of the system. The biological explanation for this phenomenon seems to be that the average population density of  $x_2$  is reduced due to competition from both  $x_1$  and  $x_3$  such that a larger predation rate is necessary for  $P_2$  to be maintained in the system. Each of the other two competitors,  $x_1$  and  $x_3$ , receives only half the competitive pressure experienced by  $x_2$ , such that a smaller predation rate is required to maintain their specialized predators in the system.

Increasing the predation rate further, a large zone of heteroclinic cycles is encountered. To visualize this modality, we take advantage of the fact that systems 1 and 3 tend to oscillate in phase, which effectively reduces them to the same system. We thus define the variables  $\Delta x$  and  $\Delta p$  as the difference between systems 1 and 3 (i.e.  $\Delta x = x_1 - x_3$  and  $\Delta p = P_1 - P_3$ ). We then examine the dynamics in  $\Delta x, \Delta p$  space, as illustrated for two cases in Fig. 4. This range of parameter space is complicated, with only two of the possible configurations illustrated in Fig. 4. There are, evidently, two alternative modalities that are repeatedly revisited either as unstable focal points or saddle cycles, qualitatively similar to the Lorenz attractor. The detailed behavior of the system in this heteroclinic zone is discussed in the next section.

Increasing the predation rate further, a zone of “uncoordinated” chaos is encountered, in which all six species are maintained in the system, similar to that reported by Huisman and Weissing (2001a). A three-dimensional plot of the competitors in this region is illustrated in Fig. 5. All attractors within this parameter zone seem to have the same general qualitative appearance. The behavior in this region is unlike the previous chaotic region in that subsystems 1 and 3 are not coordinated, but rather oscillate unpredictably with respect to one another.

In Fig. 6 we illustrate, in a bifurcation diagram, these five general behavior patterns (limit cycles with only spp 1 and 3, system 1 and 3 in limit cycle or stable focus, coordinated chaos, heteroclinic cycles, and uncoordinated chaos), color coded for four of the variables (variables 1 and 3 are qualitatively identical since the system is symmetrical, thus only the four variables are plotted).

From the point of view of the dynamics of competition we thus see two distinct forms of maintaining all three competitors in the system. First, at relatively low levels of predation intensity, a system of coordinated chaos is generated, wherein the subordinate competitor is antiphase with the two other subsystems, after having had its predator eliminated. Thus, the dynamics are effectively to have the subordinate species’ predator eliminated from the system and then generate an anti-phase cycle between the two other subsystems. Second, when predation pressure is high, the basic pattern elucidated by Huisman and Weissing (2001a) seems to be the rule, with uncoordinated chaos driving the coexistence. Between these two chaotic forms the system exhibits complicated heteroclinic cycles, which very frequently involves the elimination of the two dominant competitors, the details of which are discussed in

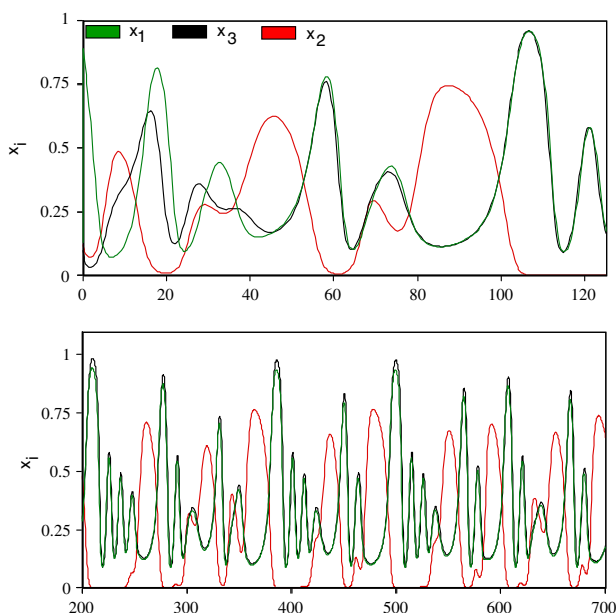


Fig. 3. Time series for all three competitors in the system. (a) Initial time series showing transients leading into the chaotic attractor. (b) From time 200 through time 700, illustrating the synchronized (coordinated) chaos of  $x_1$  and  $x_3$ , and the antiphase coordination of  $x_2$ . Note that  $x_2$  does not actually descend to the critical extinction threshold even though it may appear to do so on this arithmetic plot.



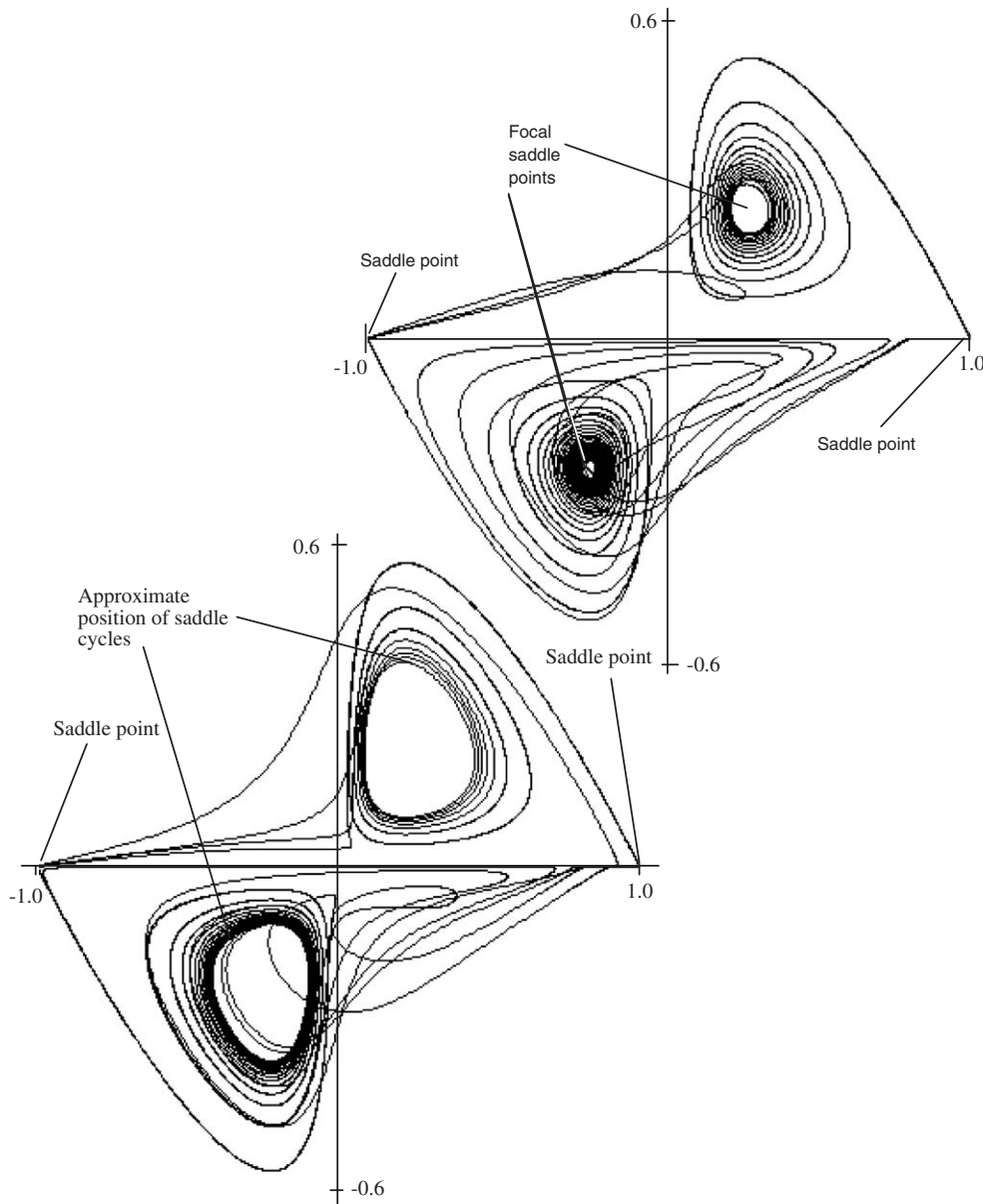


Fig. 4. Plot of  $\Delta x$  versus  $\Delta P$  (the difference between  $x_1$  and  $x_3$ , and between  $P_1$  and  $P_3$ ), illustrating two distinct forms of the heteroclinic cycle, for slightly different parameter values.

the next section. From a practical ecological perspective, the heteroclinic cycles all result in the same thing, extinction of one or more elements in the system. However, it is worth noting that elimination of  $x_2$ , the subordinate competitor, is not the first extinction event to occur in this parameter zone. Indeed  $P_2$  is inevitably the first variable to transcend the extinction threshold, as discussed in the next section. We also note, to be elaborated further in the discussion section, that since  $P_2$  is the variable that transcends the extinction barrier first, the underlying dynamics are such that, effectively, the system always reduces to the case in which the dominant competitors ( $x_1$  and  $x_3$ ) are controlled by predators while the subordinate competitor is free of predation (since  $P_2$ , its predator, is always eliminated first). Which is to say that at relatively

low levels of predation intensity, the predator specializing on the subordinate competitor will be eliminated from the system, in which case the system will inevitably be one in which the dominant competitors are controlled by predators while the subordinate competitors will be free from control from above. Thus, specialized predators do in fact have the effect of deterring the competitive exclusion of the subordinate, but through this curious biological effect of the elimination of the predatory control over the subordinate competitor. What one might expect to see in nature would be a keystone-like effect, with predators controlling dominant competitors such that subordinate competitors could remain in the system. Yet the origin of the pattern is more complicated in that there may very well be a suite of specialist predators in the system in general,



Fig. 5. Uncoordinated chaotic attractor represented in the 3D competition space.

but the specialist that preys on the subdominant competitor continues to be driven to local extinction.

#### 4. Behavior in the heteroclinic zone

An appreciation for the complexity of the dynamics of the system in the heteroclinic zone is enhanced through reference to a more tractable system initially. Kirlinger (1986) provides us with a starting point in her analytical treatment of system 1 with  $\beta = b = x_3 = P_3 = 0$ , thus reducing the 6D system to a 4D case, and eliminating the functional response. Considering only the unstable (bistable) case Kirlinger notes that in a particular parameter range the dynamics are characterized by a heteroclinic cycle. As she explains, “Biologically this means: Prey 1 is invaded by its predator, but this predator reduces the prey so much that prey 2 outcompetes it. So prey 1 dies out together with its predator, and prey 2 takes over. This lets its predator grow, which again reduces the corresponding prey. Due to bistability, the number of prey 1 increases now and so on in cyclic alteration.” When this cycle is repelling, the system becomes “permanent,” with either a focal point attractor, a limit cycle or chaos maintaining all four species in the system. However, when the cycle is attracting, all four variables approach zero asymptotically, what Kirlinger referred to as “persistent,” but which, for all practical purposes, indicates the extinction of one of the species that repeatedly approaches numbers very close to

zero. This can be seen in Fig. 7, where the logarithm of one of the competitors has been plotted. We define the parameter  $\lambda$  as,

$$\lambda = d[\ln(x_{\min})]/dt$$

where  $x_{\min}$  is a local minimum, as illustrated by the dotted line in Fig. 7 (the slope of which is  $\lambda$ ). This slope varies as a function of predator pressure (the parameter  $a$  in system 1). The approach of  $x_i$  to zero is very rapid for small predator pressure (i.e.,  $|\lambda|$  is large), becoming smaller as that pressure increases in a direct linear fashion. Thus, we find, empirically,

$$\lambda = g + ha,$$

where  $g$  and  $h$  are the parameters discussed presently. Clearly, as  $h$  decreases, the range of the parameter  $a$  that generates a heteroclinic cycle increases—as  $\lambda$  approaches zero, the heteroclinic cycle becomes repelling and the characteristic behavior in which  $x$  asymptotically approaches zero is lost, while at the other extreme, a very large absolute value of  $\lambda$  drives  $x$  to extinction so rapidly that the limits of the computer preclude computation.

We now relax one of the assumptions of Kirlinger’s model and allow  $b > 0$ , which is to say, we add functional response to the system. There is a systematic relationship between the value of  $b$  and the value of  $h$ , as illustrated in Fig. 8. While the value of  $g$  is also variable with  $b$ , it remains relatively close to  $-0.17$ , and, tentatively, can be taken as approximately constant. Thus the final computation of  $\lambda$  can be written as

$$\lambda = g + f(b)a,$$

where the shape of  $f$  is illustrated in Fig. 8b, but does not correspond to any obvious classical functional form.

Thus we see that the heteroclinic form of Kirlinger’s 4D system occupies more of the range of the parameter  $a$  as the parameter  $b$  increases, but, most importantly, the qualitative nature of the cycle remains the same.

We now consider system 1 with  $\beta = b = 0$ , but  $x_3, P_3 > 0$  (Kirlinger’s 6D system). A casual glance at the basic structure of system 1 suggests that (1) for very small predation pressure “ $a$ ”, all predators will rapidly go extinct, and  $x_2$  will be eliminated from the system through competition (assuming competition coefficients = 1.1); (2) when  $a > m$ ,  $P_1$  and  $P_3$  will enter the system, but if  $a$  is less than some critical value,  $P_2$  will not be able to enter due to the depressing effect on  $x_2$  through the competitors  $x_1$  and  $x_3$ ; (3) at some larger value of  $a$ ,  $P_2$  will become an effective predator against  $x_2$  and remain in the system. In Fig. 9 we show several time series for the log of  $P_2$ , illustrating these facts, the most important of which is that for  $a < 2.56$ ,  $P_2$  asymptotically approaches zero. However, within this zone, the rate at which  $P_2$  approaches zero is variable, gradually increasing as the parameter  $a$  increases. Furthermore, there is a critical Hopf bifurcation at some value of the parameter  $a$ , as shown Fig. 10, leading to the qualitative behavior that  $P_2$  approaches zero in an

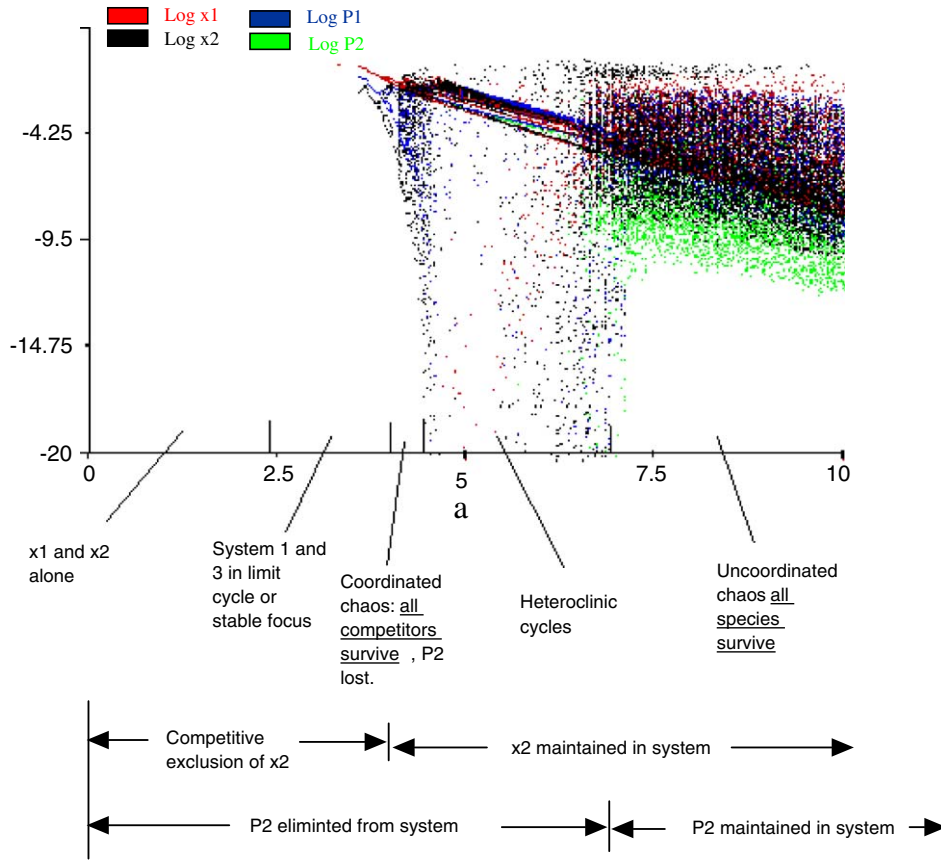


Fig. 6. Bifurcation diagram of the natural log of the local minima of four of the variables ( $P_3$  and  $x_3$  have a pattern that is qualitatively indistinguishable from  $P_1$  and  $x_1$ ), illustrating the five regions of qualitatively distinct behavior.

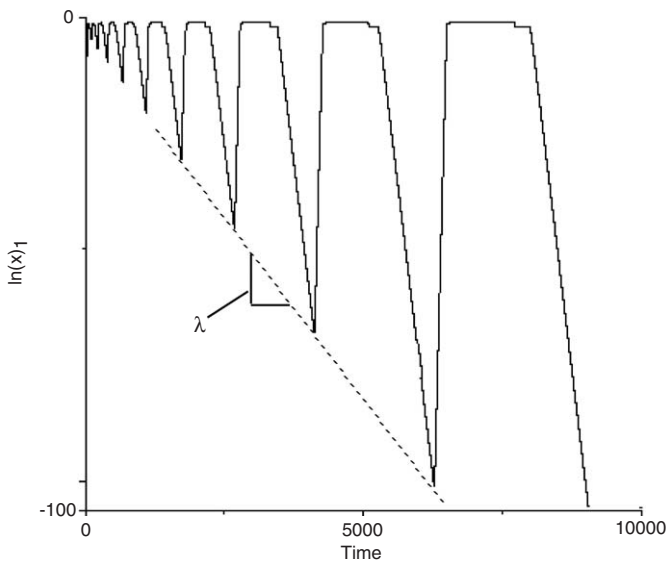


Fig. 7. Plot of natural log of one of the competitors from Kirlinger’s system, illustrating the computation of  $\lambda$ .

oscillatory fashion after the point at which a transcends that critical Hopf bifurcation point (between 2.50 and 2.55—see Fig. 9). This behavior may be related to the phenomena studied by Li and Smith (2003).

Thus, there are two (at least) qualitatively distinct behaviors exhibited by  $P_2$  in this system: (1) a heteroclinic cycle elaborated by Kirlinger (as illustrated in Figs. 7 and 8) and (2) an oscillatory asymptotic approach to zero (as illustrated in Figs. 9 and 10). The heteroclinic cycle results from the dynamics of the coupled system in four dimensions and the oscillatory approach to zero results from adding the other two dimensions to the system. The question thus arises as to how these two behaviors operate together, which they obviously must in a 6D system with  $b > 0$ . In Fig. 11 we present time series plots of the log of  $P_2$  at six values of the parameter  $a$ , with  $b$  fixed at 1.5. For these particular time series it is clear that the system moves from being dominated by the oscillatory approach to zero (Fig. 11a) to being dominated by the heteroclinic cycle approach to zero (Fig. 11f). Furthermore, the procedure of estimating  $\lambda$  is illustrated by the dotted lines in Figs. 11a and f, whereby it is clear that the unambiguous definition of  $\lambda$  (Eq. (2)) is lost. Nevertheless, the biologically significant idea of a global rate of change of the parameter as it approaches zero remains qualitatively the same as in the case of either the pure oscillatory decline (Fig. 9,  $a = 2.55$ , and Fig. 10) or the pure heteroclinic cycle (Fig. 7).

We now turn to system 1 with parameters set as in the previous section ( $m = 0.8$ ,  $b = 2$ ). Estimating  $\lambda$  for

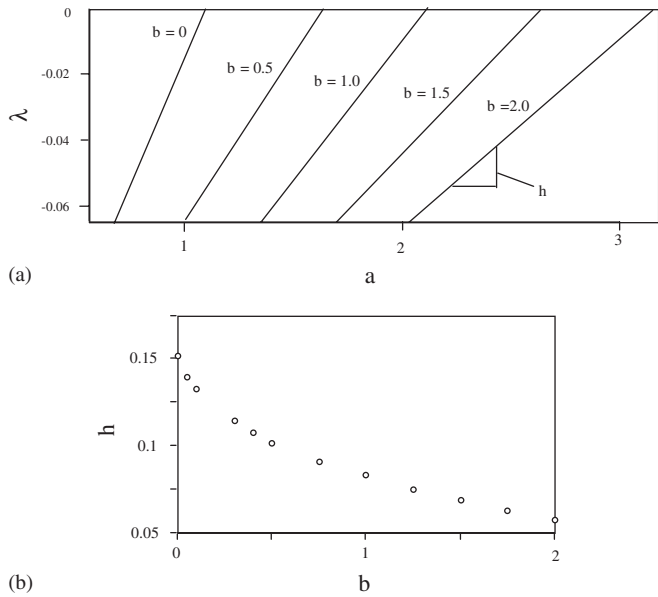


Fig. 8. Quantitative changes in  $\lambda$  as a function of parameters  $a$  and  $b$ . (a) Change in the relationship between  $\lambda$  and  $a$  as a function of  $b$ , and calculation of the parameter  $h$ . (b) Relationship between the parameter  $h$  and the parameter  $b$ .

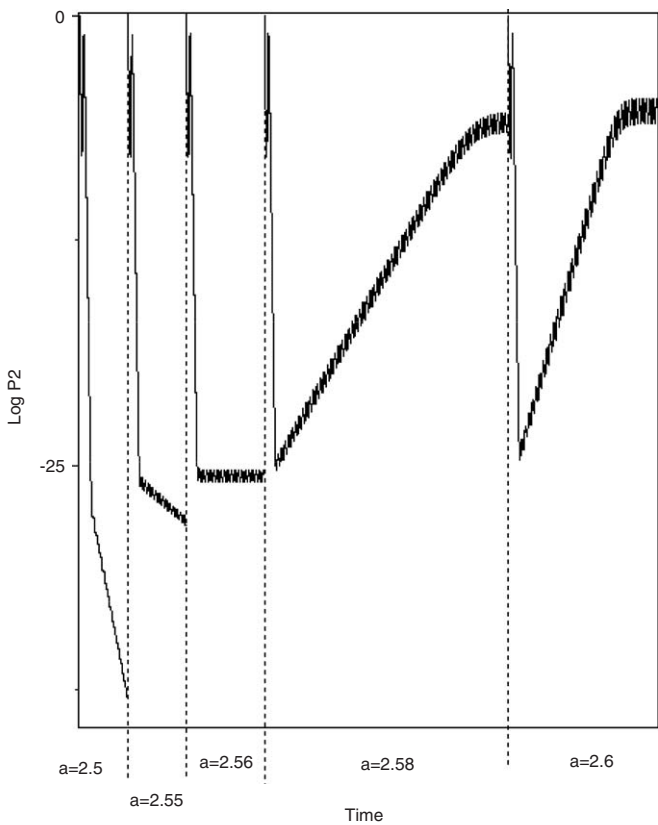


Fig. 9. Five time series for one of the variables for five different values of predator pressure (parameter  $a$ ) in Kirlinger's 6D system, illustrating first the Hopf bifurcation (between  $a = 2.5$  and  $a = 2.55$ ) and second the reversal of instability of the oscillations (between  $a = 2.55$  and  $a = 2.58$ ).

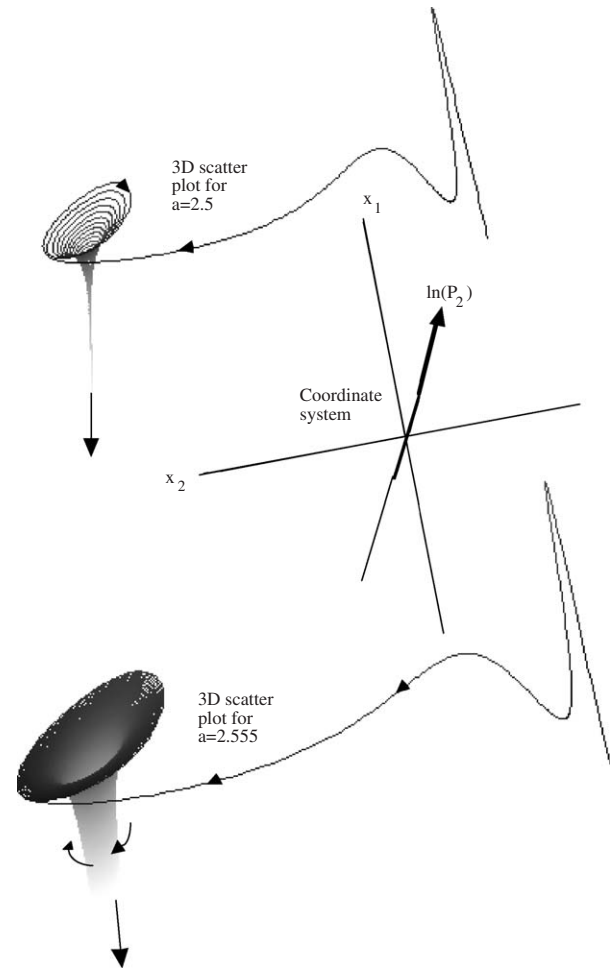


Fig. 10. The Hopf bifurcation shown in  $x_1$ ,  $x_2$ ,  $\ln(P_2)$  space. At parameter  $a = 2.5$  the system is a focal point attractor, pointing to  $P_2 = 0$ . At 2.555 the system is oscillatory, but with  $P_2$  still pointing at zero.

different values of  $a$ , we arrive at the data presented in Fig. 12. Note the abrupt change in behavior at the point  $a = 4.6$  (indicated by the dotted vertical line), where the system goes from  $\lambda$  estimated from mainly the asymptotic approach to zero to  $\lambda$  estimated from mainly the heteroclinic approach to zero. A linear regression of the latter points (the line in Fig. 12) results in the equation

$$\lambda = 0.197a - 1.37,$$

which provides an estimate of the end of the heteroclinic cycle range at  $\lambda = 0$ , or  $a = 6.95$ , which corresponds well with the observed transformation from heteroclinic to chaos (Fig. 6). There is an effective slow reversal of the stability of the heteroclinic cycle, pushing the system into a constrained but uncoordinated chaos. This basic pattern is further discussed below.

### 5. The case of generalized predators

If we now relax the assumption of complete specialization of the predators, the analysis becomes somewhat more



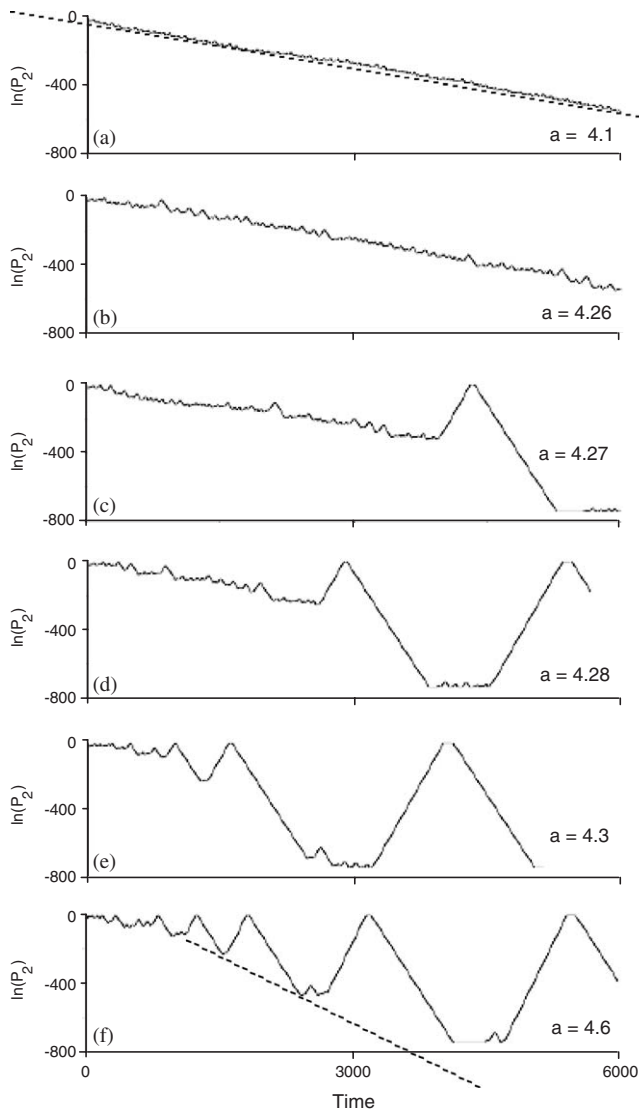


Fig. 11. Time series of the natural log of  $P_2$ , for different values of predation pressure (parameter  $a$ ) for system 1. Note the switch from a dominance of the simple oscillatory behavior ( $a = 4.1$ ) to the dominance of the heteroclinic type behavior ( $a = 4.6$ ). Dotted lines are illustrations of the calculation of  $\lambda$  (the slope of the dotted line).

complicated. As indicated in Fig. 1, we restrict the degrees of polyphagy to be internally symmetrical, which is to say the predatory effect on one non-specialized competitor is equal to the predatory effect on the other non-specialized competitor. Given this restriction, there are five qualitatively distinct cases to be analyzed, as follows: case 1,  $\beta_3 = \beta_2 = 0, \beta_1 > 0$ ; case 2,  $\beta_1 = \beta_2 = 0, \beta_3 > 0$ ; case 3,  $\beta_1 = 0, \beta_2, \beta_3 > 0$ ; case 4,  $\beta_2 = 0, \beta_1, \beta_3 > 0$ ; case 5,  $\beta_1, \beta_2, \beta_3 > 0$ . Other cases, because of the fundamental symmetry of the system, are redundant (for example  $\beta_1, \beta_2 > 0, \beta_3 = 0$  is identical to case 4).

We begin with case 1 and treat it separately from the other four cases due to its ecological significance. Much has been made in recent literature about the possible trade-off between competitive ability and vulnerability to predation

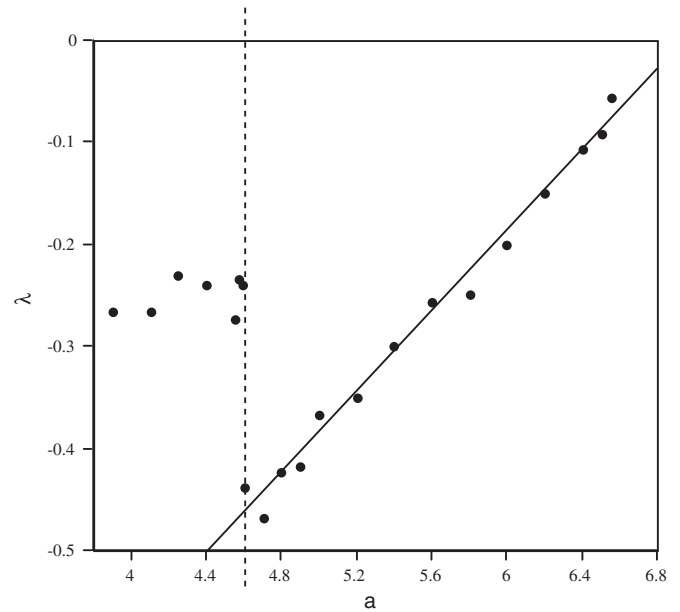


Fig. 12. Calculated values of  $\lambda$  as a function of predation pressure.

(Mills et al., 1993; Menge et al., 1994; Leibold, 1996). This is precisely what case 1 represents, with the dominant competitors ( $x_1$  and  $x_3$ ) being subjected to ever greater amounts of predator pressure, but the subdominant competitor ( $x_2$ ) subject to predation from only its own specialized predator. In this case there is polyphagy on the dominant competitors, meaning that  $P_1$  and  $P_3$  eat both  $x_1$  and  $x_3$  but not  $x_2$  the latter consumed only by its main predator. The general patterns of existence of  $x_2$  for the simple case where  $\beta = 0$ , seem to be maintained in rough outline as the polyphagy is increased (Fig. 13a), that is, the basic pattern observed for  $\beta = 0$  (as shown in Fig. 2) repeats itself as  $\beta$  increases, clearly with modifications, but qualitatively similar patterns. The exception to this generality is at high levels of  $\beta$ . Recall that  $P_2$  enters the system (i.e., is no longer necessarily eliminated through expanding oscillations) when the uncoordinated chaotic zone is encountered (compare Fig. 2 and Fig. 6). In this zone, increasing the values of  $\beta$  does cause changes in the dynamics of the system, as described presently.

Persistence or extinction of  $x_2$  is the basic topic studied in this work, and thus the black and white representations of Figs. 2 and 13a signify the answer to the fundamental question. However, as indicated in the previous sections, the dynamic patterns associated with the fate of  $x_2$  are complicated. In the case of  $\beta = 0$  those patterns were discernable (Fig. 6 and the discussion of the dynamics of the heteroclinic zone). From extensive simulations, it appears that there are nine common patterns of ultimate coexistence (assuming extinction of any population that falls below the value of  $10^{-8}$ ), as shown in Fig. 13b. There are, in fact, a variety of others, but the nine pictured in Fig. 13b appear to be the most common. Refining Fig. 13a with color coding to indicate which “mechanism” (i.e., which

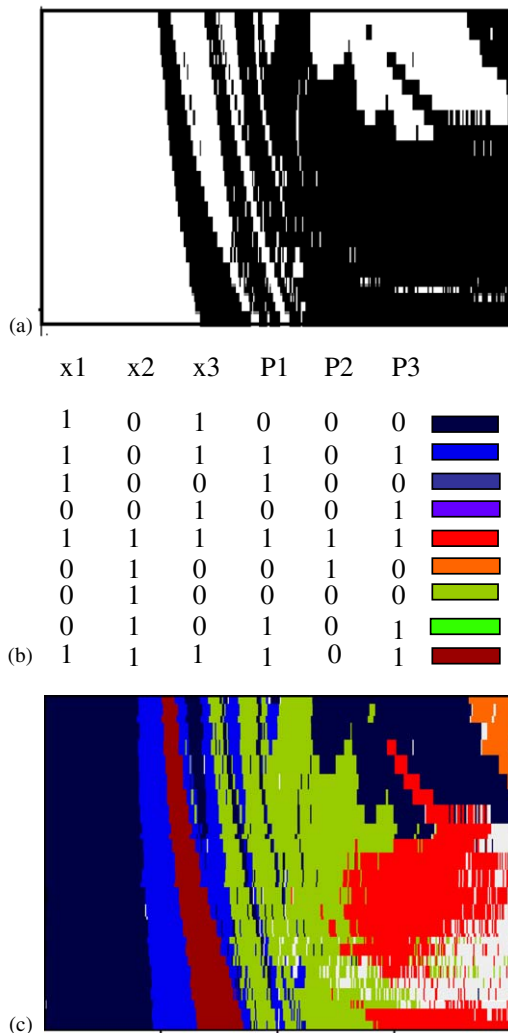


Fig. 13. Parameter space study of case 1 (trade-off between competitive ability and vulnerability to predation), plotting parameter  $a$  (abscissa) versus parameter  $\beta$  (ordinate). (a) Extinction (black) versus persistence (white) of species  $x_2$ . (b) The nine common cases (1 indicates presence, 0 indicates extinction). (c) Color coded (according to b) version of the parameter space in (a).

ultimate pattern of existence) corresponds to each state in the parameter space, we obtain the pattern displayed in Fig. 13c (note that all white spaces represent some other form of existence, not reflected in our nine-fold classification).

The underlying mechanisms are thus revealed in the color coding of Fig. 13c. When specialized predation and polyphagy are very high (upper right hand corner of Fig. 13c),  $x_1$  and  $x_3$  are reduced to a point that their predators can no longer survive due to lack of food. Consequently  $x_1$  and  $x_3$  are driven out of the system by their predators, who then follow them to extinction. Thus, the only survivors in this high predation zone are the subdominant competitor and its predator. Reducing the predatory effect (both  $a$  and  $\beta$ ) reduces the system again to  $x_2$  being eliminated by competition from  $x_1$  and  $x_3$ . Thus, generally it can be said that when the competitive ability versus predator vulner-

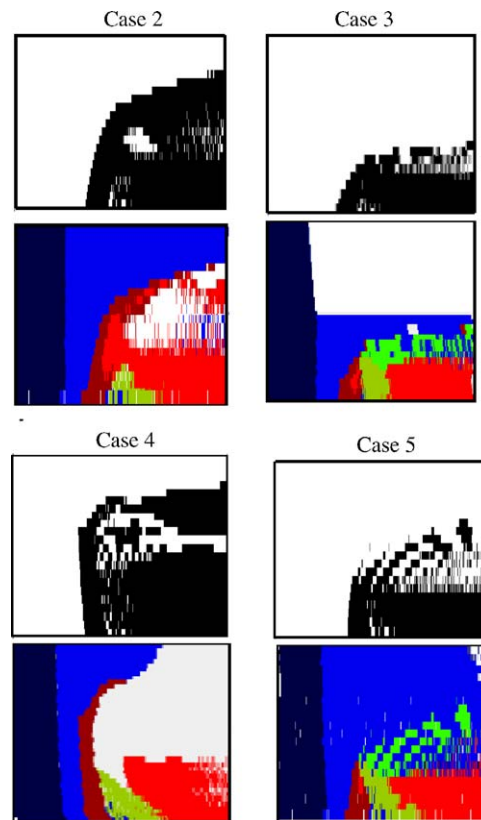


Fig. 14. Parameter space studies for cases 1–5 (see Fig. 12 for color codes), parameter  $\beta$  on ordinate, parameter  $a$  on abscissa.

ability trade-off is involved, the basic pattern of persistence of the subdominant competitor is basically the same for either specialized or generalized predation, with the important caveat that at extremely high levels of predation, the system effectively decomposes (although one pattern of that decomposition is the survival of  $x_2$ , due to the exclusion of the dominant competitors).

The other four cases of polyphagy do not fall within the rubric of the competitive ability versus predator vulnerability trade-off, and, not unexpectedly, the pattern resulting from the addition of polyphagy is distinct (Fig. 14). Cases 2–5 all have generally the same appearance, although the details vary greatly from one to another. In all cases  $x_2$  fails to survive at very high levels of polyphagy. It is also qualitatively discernable that all zones of behavior seem to qualitatively bend towards the right, more rapidly in cases 3 and 5 than in cases 2 and 4. We have not studied the detailed behavior of all of these cases, but strongly suspect that the basic patterns of behavior, as summarized above (also see Fig. 6) remain more or less constant, with a basic distortion. A particularly interesting situation arises in the parameter zones that show the light green color (in cases 3 and 5 in Fig. 14), which is the case where  $x_2$ ,  $P_1$  and  $P_3 > 0$ . The subdominant competitor coexists with the two predators that specialize on the dominant competitors, but neither the dominant competitors nor the predator that specializes on the subdominant competitor survive. This is

an unusual situation that, to our knowledge, has never been observed in nature, as we discuss more fully below.

While clear patterns associated with polyphagy can be recognized, it is nevertheless important to note that the specific way in which polyphagy is manifest (which of the five cases) in fact makes a large difference in the details of the observed pattern (Figs. 13 and 14).

## 6. Discussion

It hardly seems necessary to note that our model is a very rough “toy” model that is consequently expected to correspond to nature in a very rough way. Our results are extensions of other results (e.g., Vandermeer and Pascual, 2005) to non-symmetrical cases. As noted in that work, when relaxing symmetry in a system of multiple competitors and multiple predators, there are a very large number of ways in which asymmetry could be introduced. The present work seeks to understand the relaxation of that symmetry in a way that reflects well-known asymmetries, namely, competitors on a resource gradient and the predators that may or may not influence the competitive outcomes. Our initial expectations were that the consequences of introducing such asymmetry would be minimal, and that the simple heteroclinic cycles that seem to dominate the overall structure of symmetrical systems of predators and competitors (Vandermeer and Pascual, 2005) would likely remain relatively simple. Such was not the case, as we report herein.

Understanding the influence of predators on the competitive interactions of their prey has been a recurring theme since Darwin first talked about mowing plants. The keystone predator hypothesis, the Janzen/Connell hypothesis, and many other formulations are leitmotifs on that basic theme, even if not recognized as such. It seems obvious that if predators interfere with the competitive process, they could also defer the inevitable competitive exclusion implied by strong competition in Gause’s principle. Given the intuitively obvious importance of the idea, it is not surprising that theoreticians have weighed in on the topic (see references in the introduction). Amongst the most important of the many theoretical results already in the literature is the need for minimally the same number of specialist predators as competitors in order to deter competitive exclusion, finally proved in a general mathematical form by Schreiber (1998). On the other hand, it remains the case that generalist predators are not up to the task of changing the expected Gaussian outcome, contrary to what Darwin seems to have believed. The idea of an intermediate polyphagy, neither specialists nor generalists, was deduced from a perfectly symmetrical system (Vandermeer and Pascual, 2005). Virtually all of the theoretical musings on this problem have been concerned with a generally symmetrical system, which brings up the question as to whether a non-symmetrical system would show similar patterns.

Pursuing the general problem of predators influencing competitive outcome, if non-symmetrical, generates conceptual difficulties since there are many ways in which the symmetrical system could be made non-symmetrical. In this contribution we studied just one of those ways, one that has become common in the literature, that of three competitors on a resource gradient. This system, which in no way actually requires a truly simple one resource gradient, involves two competitors that compete at very low levels (taken here to be zero), but both of which compete at high levels with a third species. The arrangement is most easily diagrammed with the classic three competitors on a simple resource gradient, even though mathematically there is nothing that requires the system to be restricted to a simple one-dimensional gradient. The competitive relations are defined by the competition coefficients in the equations, and the position along the resource gradient is simply a convenient visual aid to see the competitive arrangements. Furthermore, since the point of the study is to examine patterns of predatory effect on the process of competitive exclusion, we restricted our analysis to strong competition between the dominants and subdominant (i.e., a competition coefficient of 1.1 which insures competitive exclusion when unperturbed).

We have studied this special case of limiting similarity and species packing in which, through the process of competition, a subdominant competitor is expected to be excluded, but through the influence of predators in the system, that exclusion may be prevented. We have demonstrated, with simple Lotka–Volterra type models, that the general consequences of adding predators to the system of one subordinate and two dominant competitors may indeed rescue the subdominant competitor (e.g., Fig. 2), as has been demonstrated previously (Hutson and Vickers, 1983; Kirlinger, 1986; Hofbauer and Sigmund, 1989; Vandermeer, 1991). However, the underlying biological reasons for this rescue effect is dramatically different for different forms of predator pressure, some of which generate complicated cycles, thus adding to the already burgeoning literature on cycles and species diversity (e.g., Abrams, 1999; Abrams and Holt, 2002; Huisman and Weissing, 1999, 2001a, b; Vandermeer et al., 2002; Vandermeer, 2004).

Given the two “dominant” competitors (those who will eliminate the subdominant absent predation) and the “subdominant” (the one that will be eliminated absent predation), the question is what will be the effect of adding predators to this competitively asymmetrical system. We approached this problem in two steps: (1) with perfectly specialist predators and (2) with various forms of asymmetry in polyphagy of the predators. Situation number one (specialist predators) was approachable through simulation experiments and led to interesting patterns of complex behavior underlying various cases of predators acting to defer expected competitive exclusion. Situation number two was far more complicated, and we

were able only to catalogue a variety of complex behavior patterns involved in deferring competitive exclusion.

In the case of perfectly specialist predators a superficial study of the system would reveal (see Fig. 1) that at low levels of predation intensity the expected competitive exclusion would continue to occur, not surprisingly since at the extreme of very little predation pressure we would expect the system to behave more or less as if predation were not present. And at the other end of the spectrum, as might be expected, the subdominant competitor escapes the competitive exclusion fate. However, the complications involved with this general and predictable qualitative result are sufficiently interesting to merit close study. First, it is obvious that at intermediate predation intensities (see Fig. 1), there is a complicated pattern in which at some values of predation intensity competitive exclusion is avoided, but at very near values, either higher or lower, it is not. Second, there exist values of predator intensity for which the subdominant competitor survives, but its specialist predator may be either present or absent. In other words, while specialist predators clearly can deter the process of competitive exclusion, something more complicated must be happening with the dynamics, which leads us to a detailed study of the dynamical patterns associated with different levels of predation intensity.

The detailed study of the specialist predator case revealed five fundamental qualitatively distinct patterns (Fig. 6). First, not surprisingly, if the predation rates are excessively small the predators go extinct and the basic Gaussian exclusion occurs. Second, as the predation rates increase, the dominant competitors and their predators coexist in either a stable focus or a limit cycle, but the subdominant still undergoes Gaussian extinction. It is not insignificant that the dominant competitors oscillate with respect to their predators.

Third, as predation pressure is increased, a parameter combination is reached in which systems 1 and 3 (i.e., the two dominant competitors and their predators) are maintained in the system, either in a stable equilibrium or a stable limit cycle, but a curious behavior is added in which systems 1 and 3 are completely in-phase coordinated with one another, with the coordination driven by the competitive interaction of  $x_2$  versus  $x_1$  and  $x_3$ . Qualitatively this behavior is perhaps to be expected, according to the following logic: Since  $P_2$  is driven out of the system in this region, what remains is the pair of oscillators  $x_1$ ,  $P_1$  and  $x_3$ ,  $P_3$ , coupled together through the competitor  $x_2$ . Since  $x_2$  connects  $x_1$  and  $x_3$  through competition between the two, the remaining predators have an indirect negative effect on each of the dominant competitors (i.e.,  $P_1$  indirectly affects  $x_3$ , because  $P_1$  negatively affects  $x_1$  which negatively affects  $x_2$  which negatively affects  $x_3$ ). By the basic topology of this connection (Vandermeer, 2004) we expect that systems 1 and 3 should be phase coordinated in synchrony, which is what is observed. It should be noted that this effect is extremely strong, and that even when the system is in chaos, subsystems 1 and 3 are still completely phase

coordinated (Fig. 3). Thus, what we have is a permanent persistence of all three competitors due to what we refer to as “coordinated chaos,” a form of chaotic coexistence that appears quite distinct from other forms (e.g., Huisman and Weissing, 1999, 2001a). Four of the six populations (the dominant competitors and their predators) oscillate chaotically, but in perfect synchrony with one another, and the remaining population (the subdominant competitor) also oscillates chaotically, but in anti-phase synchrony with the first four.

The fourth pattern (Fig. 6) occurs when the predation rate becomes yet larger, and the whole system appears to be dominated by a complicated combination of an unstable focal point or limit cycle pointed at zero (Fig. 10) coupled with a stable heteroclinic cycle. We spent considerable time analyzing this form of behavior noting that by defining a parameter,  $\lambda$ , similar to a Lyapunov exponent (not equivalent, but with similar properties), we are able to see clearly how this part of the parameter space eventually changes into other forms of chaos (see especially Fig. 12). While the details are complicated and extremely interesting from a mathematical point of view, the biological consequences are mainly that the probability of extinction in this heteroclinic zone is unpredictable, depending largely on which of the variables descends more rapidly toward zero in the general heteroclinic cycle. Thus, competitive exclusion may be avoided in this zone, but it also may go to completion, depending to some extent on the starting point. Clearly, further work on this so-called heteroclinic zone is warranted.

Finally, the fifth pattern is one of uncoordinated chaos (Fig. 5). As predation pressure increases the heteroclinic zone gives rise, suddenly, to this so-called uncoordinated chaos. This peculiar bifurcation appears to result from a reversal of the stability of the heteroclinic cycle, but retention of the instability of an internal cycle, as diagrammed in Fig. 15. The pressure away from zero caused by the unstable heteroclinic cycle is balanced by the pressure away from the internal focal point to create a zone in which the system is constrained, but nevertheless chaotic. This chaotic zone is similar to the chaotic coexistence reported elsewhere (Huisman and Weissing,

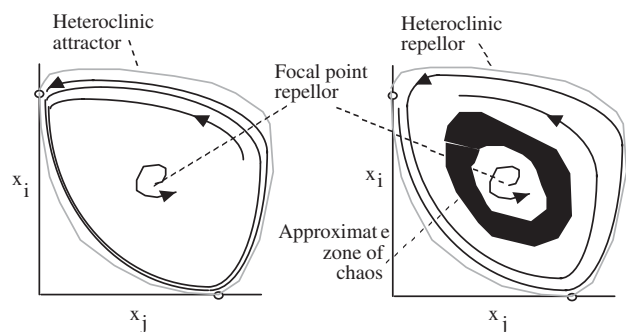


Fig. 15. Diagrammatic representation of the bifurcation from heteroclinic attractor (and ultimate extinction) to heteroclinic repeller (and chaotic coexistence).



1999, 2001a, b), perhaps with the same constraining effect of an unstable heteroclinic cycle.

This overall picture may give rise to the unusual situation (Vandermeer, 2004) in which an increase in one form of coupling has different effects depending on where the system is located with regard to some other form of coupling. For example, if the system is located in the heteroclinic zone, an increase in specialized predator pressure can result in the whole system being maintained in perpetuity, but in the form of apparently uncoordinated chaos, while a decrease in specialized predator pressure can also result in almost the whole system being maintained in perpetuity (except  $P_2$ ), but in the form of “coordinated” chaos. From the point of view of the subdominant competitor, the heteroclinic zone means an uncertain future, depending on initial conditions. Either an increase or decrease in predator pressure results in complete persistence, but in two qualitatively distinct forms—on the one hand, as an oscillatory element out-of-phase with two in-phase oscillators (e.g., Fig. 3) and absent any direct predator pressure, or, on the other hand, in chaotic fluctuations with all the other populations in the system. Such complicated behavior resulting from such a simple connection in such a simple system may be cautionary for the growing literature that seeks to understand food webs from a knowledge of the topological pattern of connections, irrespective of the qualitative nature of those connections.

When polyphagy is added to the basic system, considerable complications arise. Nevertheless, certain patterns remain evident. In the particular case of the competitive ability versus predator vulnerability trade-off (Fig. 13), the basic pattern observed in the case of specialized predators seems to be only slightly morphed, at least at relatively low levels of polyphagy. As polyphagy becomes stronger, even in this case, the pattern qualitatively changes, and  $x_2$  can be driven from the system at values of the parameter  $a$  where it was persistent with the specialist predators. However, at extremely high levels of predation (both specialized and polyphagous) the curious result emerges that the dominant systems ( $x_1$ ,  $P_1$  and  $x_3$ ,  $P_3$ ) are driven to extinction and the subdominant competitor persists, oscillating with its specialist predator. Such a result is clearly at odds with the entire idea of species packing, in that not only is the subdominant competitor rescued from exclusion, it is the only competitor to survive.

Viewing the parameter space with fuzzy glasses (Fig. 13c), it is apparent that there is a large area in which the subdominant competitor persists in the system, while all other components are eliminated (the light green coloration). Furthermore, this pattern is relatively independent of the level of polyphagy in the system—an intermediate level of specialist predation pressure (parameter  $a$ ) creates the conditions in which all but  $x_2$  is eliminated from the system. This suggests what may at first appear to be an illogical question—under what conditions can the dominant competitors persist in the system (i.e., there is no a

priori reason to expect the “dominant” competitors to be excluded)? Obviously, at low levels of predation they persist either because predation pressure is too small to defer the process of competitive exclusion, or because they are anti-phase coordinated with the subdominant competitor. On the other hand, at high levels of predation they persist in uncoordinated chaotic fluctuations with all species. At intermediate levels of specialist predation pressure, the entire system is in the heteroclinic zone and usually the oscillations of all but the subdominant competitor are sufficiently large to key-in the exclusion criterion. We thus arrive at the unusual conclusion that predation pressure can effectively reverse the competitive dominance, rendering dominant competitors excluded and the subdominant competitor surviving. This pattern is effectively the keystone predator pattern, but with the outcome due to complex population fluctuations. The underlying reason is the strong heteroclinic zone (which, as explained above, involves more than just heteroclinic cycles) that is generated by predation pressure.

In polyphagous systems that do not involve the trade-off between competitive ability versus predator vulnerability (Fig. 14), the situation is more complex, but generally follows a similar pattern among these four cases. The subdominant competitor may be maintained in the system at low levels of polyphagy, but is inevitably eliminated when polyphagy reaches a higher level. Furthermore, there is a general pattern of each of the zones of dynamic behavior “bending” to the right as polyphagy increases. However, despite these generalizations, the details of the dynamic behavior are complicated, with obvious alternative basins of attraction occurring in a variety of places in the parameter spaces, along with complex patterns of chaos that we have not attempted to analyze completely.

A particularly interesting case is observed in the uncoordinated chaotic zone of cases 3 and 5. As both  $\beta$  and  $a$  increase, the heteroclinic zone that gives rise to  $x_2$  alone surviving (light green in color) appears to give rise to complex oscillations (seemingly chaotic) involving  $x_2$ ,  $P_1$  and  $P_3$ . The dominant competitors as well as the predator of the subdominant have been eliminated from the system and what remains is an oscillatory system involving the subdominant competitor along with the predators that do not specialize on it, and in the absence of the main food sources of those two predators.

Finally, it is worth noting that while we begin with an obvious and well-studied situation, that of three competitors on a gradient affected in various ways by predators in the system, the ultimate results are remarkably complicated (Figs. 13 and 14), and include situations that, if encountered in nature, would never cause suspicion that they were derived from the basic and obvious setup. Thus, for example, the case where  $x_2$ ,  $P_1$  and  $P_3$  survive in perpetuity, if encountered in nature would seem to be nothing more than two predators surviving on a single competitor (e.g., the case of Armstrong and McGehee, 1980), rather than the outcome of the original six-species system. In this sense,

each of the outcomes in Figs. 13 and 14 can be considered as a particular community assembly. However, from this point of view, we can hardly ignore the existence of many alternative community structures, the nine depicted in Fig. 13, plus many more not explicitly shown here (which are included in the white areas in the color panels of Figs. 13 and 14). These alternative structures depend both on position in parameter space and, depending on that position, on the initial values of the populations.

## References

- Abrams, P., 1983. The theory of limiting similarity. *Ann. Rev. Ecol. and Syst.* 14, 359–376.
- Abrams, P., 1999. Is predator-mediated coexistence possible in unstable systems? *Ecology* 80, 608–621.
- Abrams, P.A., Holt, R.D., 2002. The impact of predator–competitor cycles on the coexistence of competing predators. *Theor. Popul. Biol.* 62, 281–295.
- Armstrong, R.A., McGehee, R., 1980. Competitive exclusion. *Am. Nat.* 106, 220–236.
- Bakker, E.S., Olff, H., 2003. Impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grasslands. *J. Veg. Sci.* 14, 465–474.
- Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Ann. Rev. Ecol. Syst.* 31, 343–368.
- Connell, J.H., 1971. In: den Boer, P.J., Gradwell, G.R. (Eds.), *Dynamics of Populations. Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations.* Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands, pp. 193–312.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Cordeiro, N.J., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proc. Natl. Acad. Sci. USA* 100, 14052–14056.
- Cramer, N.F., May, R.M., 1972. Interspecific competition, predation and species diversity: a comment. *J. Theor. Biol.* 3, 289–293.
- Darwin, C., 1998. *The Origin of Species.* Modern Library Paperback Edition, Random House, NY.
- de Roos, A.M., McCauley, E., Wilson, W.G., 1991. Mobility versus density-limited predator–prey dynamics on different spatial scales. *Proc. R. Soc. London B* 246, 117–122.
- de Roos, A.M., McCauley, E., Wilson, W.G., 1998. Pattern formation and the spatial scale of interaction between predators and their prey. *Theor. Popul. Biol.* 53, 108–130.
- Fujii, K., 1977. Complexity–stability relationship of two-prey one-predator species system model: local and global stability. *J. Theor. Biol.* 69, 613–623.
- Harper, J.L., 1996. The role of predation in vegetational diversity. *Diversity Stability Ecol. Syst. Brookhaven Symp. Biol.* 22, 48–62.
- Hofbauer, J., Sigmund, K., 1989. On the stabilizing effect of predators and competitors on ecological communities. *J. Math. Biol.* 27, 537–548.
- Hsu, S.B., 1981. Predator-mediated coexistence and extinction. *Math. Biosci.* 54, 231–248.
- Huisman, J., Weissing, F.J., 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 401, 407–410.
- Huisman, J., Weissing, F.J., 2001a. Biological conditions for oscillations and chaos generated by multispecies competition. *Ecology* 82, 2682–2695.
- Huisman, J., Weissing, F.J., 2001b. Fundamental unpredictability in multispecies competition. *Am. Nat.* 157, 488–494.
- Hutchinson, G.E., 1948. Circular casual systems in ecology. *Ann. NY Acad. Sci.* 50, 221–246.
- Hutson, V., Vickers, G.T., 1983. A criterion for permanent coexistence of species with an application to a two-prey one-predator system. *Math. Biosci.* 63, 253–269.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528.
- Kinzig, A.P., Levin, S.A., Dushoff, J., Pacala, S., 1999. Limiting similarity, species packing, and system stability for hierarchical competition-colonization models. *Am. Nat.* 153, 371–383.
- Kirlinger, G., 1986. Permanence in Lotka–Volterra equations: linked predator–prey systems. *Math. Biosci.* 82, 165–191.
- Leibold, M.A., 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.* 147, 784–812.
- Leibold, M.A., 1998. Similarity and local co-existence of species in regional biotas. *Evol. Ecol.* 12, 95–110.
- Li, B., Smith, H.L., 2003. Periodic coexistence of four species competing for three essential resources. *Math. Biosci.* 184, 115–135.
- MacArthur, R.H., 1970. Species packing and competitive equilibria for many species. *Theor. Popul. Biol.* 1, 1–11.
- MacArthur, R.H., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101, 377–385.
- Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr.* 64, 249–286.
- Mills, C.S., Soule, M.E., Doak, D.F., 1993. The keystone species concept in ecology and conservation. *BioScience* 43, 219–224.
- Pacala, S.W., Tilman, D., 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am. Nat.* 143, 222–257.
- Paine, R.T., 1974. Intertidal community structure, experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15, 93–120.
- Parrish, J.D., Saito, S.B., 1970. Interspecific competition, predation and species diversity. *J. Theor. Biol.* 27, 207–220.
- Roughgarden, J., Feldman, M., 1975. Species packing and predation pressure. *Ecology* 56, 489–492.
- Ryerson, D.E., Parmenter, R.R., 2001. Vegetation change following removal of keystone herbivores from desert grasslands in New Mexico. *J. Veg. Sci.* 12, 167–180.
- Schmitz, O.J., 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol. Lett.* 6, 156–163.
- Schreiber, S.J., 1997. Generalist and specialist predators that mediate permanence in ecological communities. *J. Math. Biol.* 36, 133–148.
- Schreiber, S.J., 1998. On the stabilizing effect of specialist predators on founder-controlled communities. *Can. Appl. Math. Quart.* 6, 195–206.
- Spiller, D.A., Schoener, T.W., 1990. Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia* 83, 150–160.
- Vandermeer, J.H., 1991. Contributions to the global analysis of the Lotka–Volterra equations: a system of two prey and a predator. *J. Theor. Biol.* 148, 545–561.
- Vandermeer, J.H., 2004. Coupled oscillations in food webs: balancing competition and mutualism in simple ecological models. *Am. Nat.* 163, 857–867.
- Vandermeer, J.H., Pascual, M., 2005. Coexistence through intermediate polyphagy. *Ecol. Complexity* (in press).
- Vandermeer, J., Evans, M.A., Foster, P., Höök, T., Reiskind, M., Wund, M., 2002. Increased competition may promote species coexistence. *Proc. Natl. Acad. Sci. USA* 99, 8731–8736.
- Yodzis, P., 1995. In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Patterns and Dynamics.* Kluwer Academic Publishers, London, pp. 192–200.