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Competitive coexistence through intermediate polyphagy

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ABSTRACT

Communities containing species that are not niche differentiated require some mechanism to avoid the expected competitive exclusion of all but one or a few species. Predator pressure has long been held to be one of those mechanisms. Here, we show that the critical feature of predation is not its intensity, but its degree of specialization. Neither highly specialist nor highly generalist predators are effective at deterring competitive exclusion, but rather predators that exhibit an intermediate level of polyphagy can effectively provide such a mechanism.

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1. Introduction

Competition occupies a central place in modern ecological theory. There are generally two extremes on a continuum of thinking about how communities are organized by this process, niche-oriented versus non-niche-oriented (Wills et al., 1997). At one extreme some communities are thought to be organized through niche differences such that competition among species is sufficiently weak to allow for coexistence (MacArthur, 1970; Levine, 1976; Grubb, 1977; Pacala and Tilman, 1993; also referred to as equilibrium communities, Connell, 1978; or dominance-controlled communities, Yodzis, 1989). At the other extreme some communities are thought to contain species that effectively occupy the same or similar niches, such that they would be expected to eliminate one another eventually (Hubbell and Foster, 1986; Silvertown and Law, 1987, also referred to as non-equilibrium communities, Connell, 1978; or founder-controlled communities, Yodzis, 1989). This latter point of view was immortalized in the observations of Hutchinson popularly known as the “paradox of the plankton” (Hutchinson, 1961). Several kinds of diverse assemblages of species, from rain forest trees to phytoplank-

ton have been postulated as possibly falling into this category, with competition coefficients large enough to cause eventual extinction of all but a single species, either through active competitive exclusion or, in the case of perfectly equivalent species, through random drift. It is the latter type of community (non-niche, or non-equilibrium, or founder-controlled) that we analyze in this paper, taking the extreme situation in which a suite of competitors have competition coefficients large enough to insure the extinction of all but one species, in a purely competitive situation.

It has long been thought that one way of stabilizing such an inherently unstable competitive assemblage of species is with predatory pressure (Chase et al., 2002). It seems intuitively compelling that a predator or a suite of predators (or herbivores or parasites) could reduce competitive pressure and thus allow what would seem to be an unstable community to become stable. We refer to this idea as the natural enemies hypothesis. This hypothesis takes many forms, from observations of Darwin (1998) (also see Van Valen, 1974), to an explicit statement by Hutchinson (1948), to the classic experiments that established the central idea of the keystone predator (Paine, 1974), to experiments with herbivores in grasslands

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(Harper, 1969; Ryerson and Parmenter, 2001; Bakker and Olf, 2003), to the so-called “Janzen/Connell hypothesis” (Janzen, 1970; Connell, 1971) to more recent work with more complicated food webs (Spiller and Schoener, 1990; Yodzis, 1995; de Roos et al., 1991, 1998; Vandermeer et al., 2002) and the implied top down effect of predators on a lower trophic level (e.g., Schmitz, 2003). Recently, a variant of the basic idea has been proposed as a partial explanation for the hyper-diverse communities of tropical rain forests (Wills, 1996). A key component in much of this literature, although not necessarily explicitly recognized as such, is the degree of specialization or generalization in the food habits of the predators of concern (Levine, 1976).

Mathematical theory has been employed to demonstrate the natural enemies effect at least since 1970 where computer simulations suggested that a generalist predator could not stabilize a two-species bistable competitive system (Parrish and Saito, 1970). Subsequent analytical work (Cramer and May, 1972; Fujii, 1977; Vance, 1978; Hsu, 1981; Vandermeer, 1991) demonstrated that indeed a generalist predator, under certain parameter combinations, could stabilize two or more competitors that would otherwise compete one another to extinction. All of these examples were in the context of either a single stable equilibrium, or one of the competitors dominating the other, but never the bistable case. Most important for the present work are the results of Hutson and Vickers (1983) demonstrating that a single generalist predator cannot convert an unstable (bistable) two-species competitive system to a stable one. The competitive system considered in this paper is inherently unstable, or multistable, in the sense that only one of a group of competitor species will survive in perpetuity in the absence of predation. The extension of Hutson and Vickers’ result to a multi species case demonstrated that a generalist predator would be unable to deter the process of competition in an inherently unstable case (Schreiber, 1997, 1998; Butler and Wolkowicz, 1986; Wolkowicz, 1989). On the other hand, Kirlinger (1986) was able to show that two properly chosen specialist predators could stabilize an unstable pair of competitor species, suggesting that it was the generalist nature of the predator in Hutson and Vickers’ model that disabled the controlling effect of predation, an important observation for the results of the present communication. Finally, Schreiber (1997, 1998) generalized Kirlinger’s result to n -species, demonstrating that a minimum of n specialist predators are required to reverse competitive exclusion of n competitors in a non-equilibrium (non-niche, founder-controlled, multistable) situation. Several authors have noted the importance of repelling heteroclinic cycles in this predator control dynamic (Kirlinger, 1986; Schreiber, 1997, 1998).

Here, we add to this body of theoretical work by examining the case of multiple competing species located intermediate on the continuum formed by complete generalization versus complete specialization of predators. It is the case that, for a particular range of parameter values, neither completely specialist nor completely generalist predators are able to maintain a species-rich assemblage of prey when competition is strong among the prey species. However, for those same parameter values, the potential of predators to maintain a species-rich assemblage of prey depends on the polyphagous

nature of the predators, with an intermediate level of polyphagy providing that maintenance service. Furthermore, under these circumstances, the transition from maintenance of a large number of the competitors together, to the exclusion of all but one, is accompanied by a critical bifurcation of a heteroclinic cycle from repelling to attracting, as explained below.

2. The model and results

Assume that each competitor is preyed upon by a particular predator, but the predator is able to consume alternative species at some rate that is smaller than the rate at which it consumes its specialist prey. Thus, a system of many competitors and their predators may be thought of as a series of predators using a suite of weighted competitors, θ all of which are competing with one another. Hence,

$$\theta_i = x_i + c \sum x_j$$

where the summation is over all $j \neq i$, x_i is the density of the i th competitor, c the conversion factor that converts a unit of competitor j into a unit of predator i , where $0 < c < 1.0$. In other words, the populations consumed by a particular predator are a collection composed of a principal competitor plus a series of other competitors that are consumed in proportion to the consumption of the principal competitor (i.e. c). Thus, the parameter c is the “degree of polyphagy” of the predators. To be clear, when $c = 0$, all predators are specialist, when $c = 1$ all predators are generalists, and when $0 < c < 1$, all predators are intermediate, which is to say, polyphagous, with an intermediate degree of specialization.

If θ_i represents the competitors that are prey for the i th predator, the dynamic equations can be written in standard Lotka–Volterra (with density dependence and type II functional response) form as:

$$\frac{dP_i}{dt} = -mP_i + \frac{a\theta_i P_i}{1 + b\theta_i} \quad (1a)$$

$$\frac{dx_i}{dt} = x_i \left(1 - x_i - \alpha \sum x_j \right) - \left[\frac{ax_i P_i}{1 + b\theta_i} \right] - ac \sum \frac{x_i P_i}{1 + b\theta_j} \quad (1b)$$

where P_i is the density of the i th predator, a the predation rate, m the mortality rate of the predator, b the parameter of the functional response, α is the competition coefficient, and the summation is taken over all $j \neq i$, for $j = 0, 10$. This way of writing the functional response for multiple species is chosen as a direct extension of the form normally used for a single species, where, instead of a single competitor generating the response, we use the “effective” competitor (i.e. θ), and employ a type II functional response. If b and α are set to zero, system 1 becomes equivalent to the extended Lotka–Volterra system with simple density dependence—all solutions are simple focal point attractors and, assuming that $\alpha < m$, extinction is impossible for any c (in the range 0–1).

However, if b is set sufficiently large (keeping $\alpha = 0$) such that all uncoupled two-dimensional subsystems (any predator/competitor pair) exhibit limit-cycle behavior, a substantially different pattern is observed when the parameter c is increased. As c becomes larger, eratic cycles may be generated

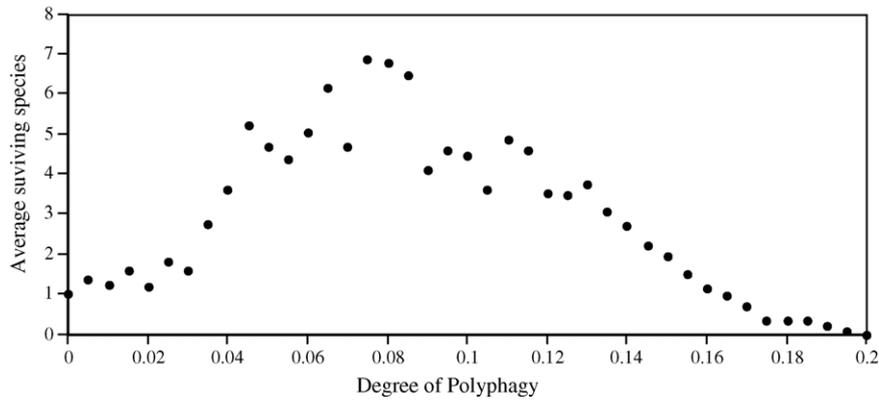


Fig. 1 – Average number of coexisting competitors as a function of the specialization of the predators, based on system 1. Parameter values are $m = 0.8$, $b = 1.5$, $a = 15$. Iterations were carried out to 1000 time steps. The critical minimum value for persistence is 10^{-6} .

in which both competitor and predator can become so small that their extinction from the system is virtually assured through a very small stochastic effect. Under such circumstances, it must be assumed that there is some critical lower boundary to the size of the population, such that any population dipping below that critical value can be thought of as essentially extinct. To simulate this extinction force, the critical lower limit at which a population is regarded as extinct was set at 10^{-6} , that is, allowing a population density range of 0 to 100,000.

When c is equal to zero (perfectly specialist predators), and $\alpha = 1.1$, for all parameter values investigated in this study ($a = 0-40$, in intervals of .04, $b = 0-4$, in intervals of .008) the system generates extinction of all but one competitor. Clearly, there are other parameter values for which coexistence is possible, as demonstrated by Kirlinger (1986), who provides precise conditions for such a stabilizing effect for both a four species and six species system (two predator prey pairs and three predator prey pairs), and Schreiber (1997, 1998) who provides those precise conditions for n -species. We studied the part of the parameter space in which completely specialist predators did not change the ultimate conclusion of competitive exclusion.

At the other end of the spectrum, with c equal to 1.0 (defined as completely generalist predators), there is also a complete elimination of all but one competitor, a well-known result (Schreiber, 1997, 1998). Thus, for a wide range of parameter values (a and b), neither perfectly specialist nor perfectly generalist predators change the inevitable Gausean outcome of elimination of all but one of the competitors (α , the competition coefficient, is always 1.1 in these simulations, assuring the elimination of all but one of the competitors). Thus, for the parameter values studied here, the predators apply added negative pressure to each of the competitor populations such that all but one disappears.

However, even when parameters are such that neither specialist nor generalist predators are able to deter competitive exclusion (as in the cases studied here), the introduction of an intermediate degree of polyphagy (intermediate values of c) results in a different pattern (Fig. 1). Many or all competitors coexist in a window of intermediate polyphagy.

For the particular example chosen in Fig. 1, this window is when c is approximately between 0.03 and 0.16. This example suggests that the only way in which predators could act to deter the ultimate complete competitive exclusion, is if there is an intermediate amount of polyphagy in the system.

The underlying mechanism giving rise to this pattern can be intuitively seen by eliminating the critical minimum that generates extinction and graphing the minimum of any of the competitors as a function of the degree of polyphagy, as has been done in Fig. 2. There is a clear transition at approximately 0.3 (most clearly visible in Fig. 2b), at which a heteroclinic cycle seems to appear for all higher values of polyphagy. The heteroclinic nature of the trajectories can be seen in a time series, as shown for all 11 competitor species in Fig. 3. After the initial 8000 iterations (Fig. 3a), the typical pattern is for one species to dominate while all others remain very close to zero, only to be replaced by other species which then dominate for a while, which are then replaced by others, and so forth. Fig. 3b

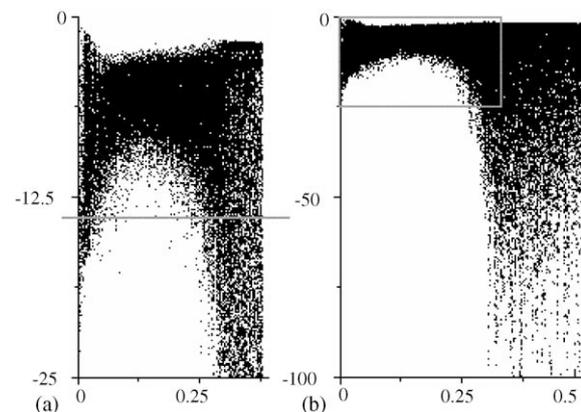


Fig. 2 – Bifurcation diagram of the minima of the log of x_3 as a function of degree of polyphagy (c) from system 1. Parameters as in Fig. 1 except there was no critical minimum for persistence. (a) Limited range of log of x , showing position of critical extinction line (dotted horizontal line). (b) Expanded range of log of x showing the critical heteroclinic bifurcation. Dotted rectangle in (b) is the area represented in (a).

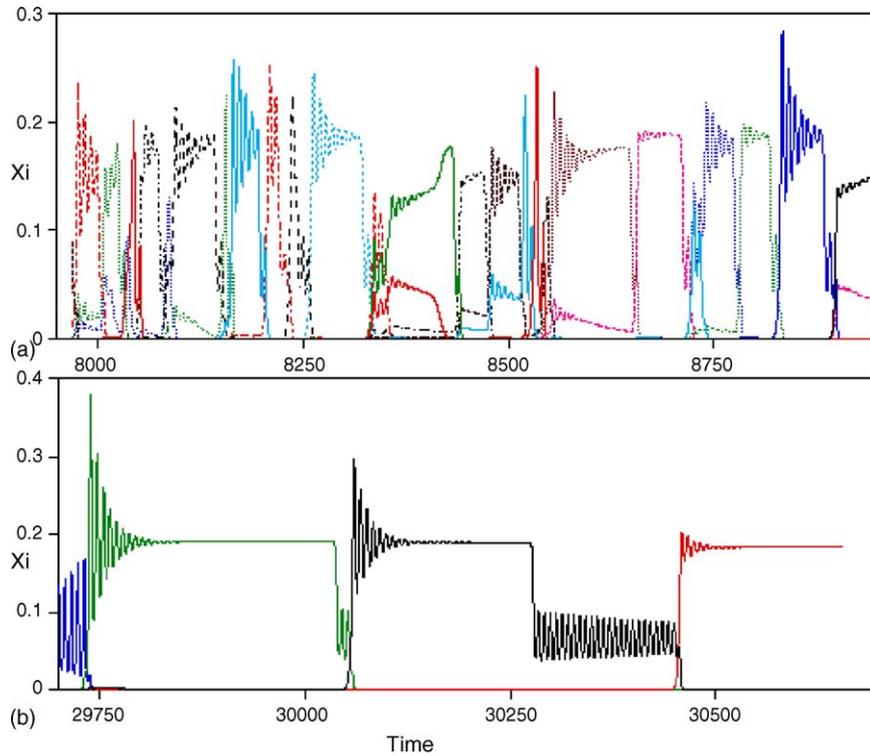


Fig. 3 – (a) Time series for all 11 competitors in the 22 species system, with $c = 0.35$. (b) Same time series for later iterations. Parameter values as in Fig. 1.

shows the same time series after 30,000 iterations. The time that one species predominates is now much longer than at earlier times in the simulation, indicating that the system is approaching a heteroclinic cycle and thus lingers near each focal saddle point for an ever longer period of time. This pattern continues, as far as we can tell from these numerical solutions.

To the left of the bifurcation point that results in the heteroclinic cycle (see Fig. 2a), the system is apparently in chaos, although constrained by the remnants of the same heteroclinic cycle (Huisman and Weissing, 2001). These dynamic patterns explain the origin of the coexistence window in Fig. 1. By choosing some critical value of the minimum allowable population (in this case 10^{-6} , as indicated by the dotted horizontal line in Fig. 2a), the size of the coexistence window can be chosen from Fig. 2, but only within the limits of the heteroclinic bifurcation, that is, the limits of the window can never extend to the right of that bifurcation, for, no matter how small the critical value chosen, it will always be transcended since all population trajectories approach zero asymptotically.

3. Visualizing the heteroclinic cycle in lower dimension

The basic heteroclinic cycle can be visualized in a special four-dimensional form. Consider the four-dimensional system formed by allowing $x_i = P_i = 0$ for $i = 2, 10$, which is to say only the first and second ($i = 0, 1$) predator/prey exist. We now examine the system with $c = 0.375$, a value chosen to be within

the zone of heteroclinic orbits. In many locations in parameter space (including the particular point examined here) the system appears to oscillate between domination of the x_1, P_1 subsystem and domination of the x_2, P_2 subsystem, interspersed with a close approach to extinction of one or the other

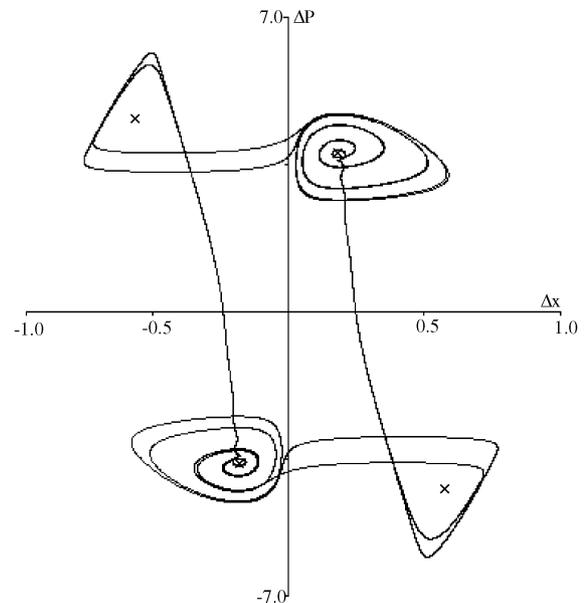


Fig. 4 – Phase space of four-dimensional system projected onto the ΔP vs. Δx space where Δ refers to the difference between the two variables (either P_1 vs. P_2 or x_1 vs. x_2). Parameters the same as in Fig. 3 with $c = 0.375$.

of the x_i . In such cases, we can visualize this four-dimensional system in two dimensions with the following transformations:

$$\Delta x = x_1 - x_2, \quad \Delta P = P_1 - P_2.$$

In Fig. 4, we present the trajectory for system 1 with $c = 0.375$ plotted as Δx versus ΔP , where the expected pattern of a heteroclinic cycle is evident (note that in Fig. 4 there are four saddle singularities, each identified with a small x , but two of those are oscillatory saddles).

4. Discussion

In a recent review (Chase et al., 2002), it is concluded that Yodzis (1986) got it right, in that simple models dealing with predatory effects on competition show that predation “can have positive, negative or no effect on coexistence,” perhaps a less than satisfying conclusion. However, the enormous literature on this topic includes an extensive mix of special conditions (e.g., a trade-off between predator vulnerability and competitive ability or predator switching or spatial dynamics; Sommer and Worm, 2002), which makes it unsurprising that almost any result is possible depending on how the problem is formulated (Chase et al., 2002). Here, a very special case is treated, in which all competitors are equivalent and compete with one another very intensely—the competition coefficients are set at 1.1 so as to insure complete extinction of all but one species in the absence of predation. Given this assumption, it is shown that, for certain parameter combinations, the critical feature of the predation is not its intensity, but its degree of specialization. Under these conditions, neither of the two extremes of completely specialist predators nor extremely generalist predators (effectively, a single predator that eats all competitors equally) is effective at deterring competitive exclusion. Rather, an intermediate level of polyphagy functions to reduce the number of extinctions due to competition. This result emerges from the cycling nature of the predator/prey systems, reflecting recent, perhaps surprising, results that emerge from adding extra non-linearities (e.g., functional response) to the basic Lotka Volterra system (e.g., Armstrong and McGehee, 1980; Abrams, 1999; Abrams and Holt, 2002; Vandermeer et al., 2004).

These results have an indirect bearing on previous reports concerning weak links in food webs (McCann et al., 1998; Neutel et al., 2002). The “links” in the food web under study here are, effectively, the competition coefficients (which are set constant at 1.1), the rate at which the specialist competitor is consumed (which is set equal to $a = 15$ here), and the rate at which the alternative competitors are consumed (c , varying from 0 to 1). The weak connections in this food web are thus the connections between predators and their alternative competitors, equal to the value of c . It is found that small values of c can cause an otherwise non-persistent system to become persistent in perpetuity (the window of coexistence at low values of c). This then is another example of weak connections “stabilizing” food webs, lending a note of further generality to previous observations (McCann et al., 1998).

It is possible to provide an intuitive explanation for these results from the point of view of a single competitor species

(Fig. 4). The predator consumes its main prey at some rate (label a —the bold arrow in Fig. 4). If that rate is large relative to the rate at which the alternate competitors are consumed (label c in Fig. 4), the prey either becomes very scarce and the predator is unable to obtain sufficient quantities of it to survive, or the prey itself is directly driven to extinction by the predator. At the other extreme, if polyphagy is strong (label c in Fig. 4 approaches a), the predators exert downward pressure on all the competitors and the competitors are excluded due to this added effect. As the general pool of competitors becomes scarce, the predators are excluded, one by one. Between these two extremes is a zone of balance between direct exclusion of the principal prey and direct exclusion of all prey, where neither pattern dominates and there is a sort of indirect mutualism (Vandermeer, 1980) where the predator has a negative effect on the alternate prey which in turn have a negative effect on the principal prey, thus leading to a net indirect positive effect of the predator on the principal prey (Vandermeer, 2004). Thus, there are three patterns that might be expected: (1) competitor species are excluded because of overexploitation by their specialist predator, and subsequently predator species are excluded due to loss of their principal food source, followed in turn by competitive exclusion of competitor species (when polyphagy is small and the interaction labeled “ a ” in Fig. 5 is dominant), or (2) competitor species are generally excluded due to downward pressure from all predators, followed by exclusion of predator species, and later exclusion of remaining competitor species through competition (when polyphagy is large and interactions a and c are dominant), or (3) all species are maintained in perpetuity (when the indirect interaction symbolized as the combination of c and α in Fig. 4 dominates over the direct effect of a and c).

A more mathematical interpretation of these results is suggested from the qualitative behavior of the heteroclinic cycle. Consider the case of a relatively large amount of polyphagy, such that the system is in its heteroclinic phase (i.e. to the right in Fig. 2b). As polyphagy is reduced, the attraction of the heteroclinic cycle is reduced, and eventually reaches a bifurcation point at which the heteroclinic cycle becomes repelling (the obvious switch in behavior of the system at $c =$ approximately 0.34). However, there is at least one internal repeller that remains in the system, such that there is pressure away from the boundaries (i.e. the zero

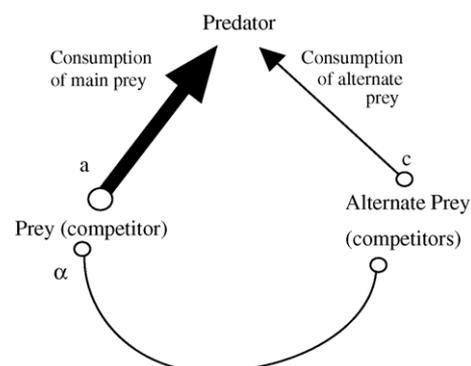


Fig. 5 – Qualitative conceptualization of the dynamics (system 1) (see text for explanation).

values on all axes) caused by the repelling heteroclinic cycle, but pressure outward (i.e. toward the boundaries) caused by the internal repeller(s). The balance of these two forces creates a zone of chaos that has a restricted lower boundary. Further reduction in polyphagy increases the strength of the internal repeller relative to the repelling heteroclinic cycle, causing the oscillations to become more extreme.

These results could obviously change if some of the simplifying assumptions imposed on the system are relaxed. For example, in the basic formulation there is no provision for density-dependent switching of prey type. A type III functional response that would result from switching could modify the general result. Another simplification is the mean field approach, which ignores the explicit nature of space (Durrett and Levin, 1994, 1998; Pascual et al., 2001; Caswell, 1978). In fact the above cited proposition of Wills was formulated with an explicit reference to space. Repeating the analysis presented here with a spatially explicit model would be of great interest, but has not yet been done.

Another issue of concern is the symmetry of the whole system. Beginning with the symmetrical case seemed to be the most rational approach, even though perfect symmetry obviously never exists in nature. However, relaxing the assumption of symmetry is not an obvious exercise since there are a wide variety of qualitatively distinct ways of doing so. At the most obvious level, each of the parameters in the system could be given variance. Thus, for the parameters a and b , simulation experiments indicate that with a range of $a = 14 + 0.2i$, and $b = 1 + 0.5i$ (where i is the index value of one of the species and varies from 0 to 10), the qualitative results reported in this paper are only very slightly modified. It cannot be said how a larger variance of these parameters might change the results, a subject for further study. However, for these deviations from the perfectly symmetrical case, our results are virtually unchanged. Nevertheless, it is also the case that the connections made through the parameter c could take a variety of forms. For instance, with c taking on a binary condition of either greater than 0 or equal to zero, the number of qualitatively distinct possibilities of making the polyphagy connections is enormous. Studies are currently underway examining these qualitatively distinct forms of polyphagy for a six species situation (three predators and three prey), in which the competitors form a competitive chain (two dominant and one subordinate competitor) and there are only two omnivorous connections (Vandermeer et al., 2004). Even with such restrictions, this case provides us with five qualitatively distinct arrangements and is surprisingly resistant to generalization. Clearly such questions are important and are under investigation currently, but certainly it is important to understand the "base line" case, the case of perfect symmetry.

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