

Omnivory and the stability of food webs

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Abstract

The ecological concept of omnivory, feeding at more than a single trophic level, is formulated as an intermediate stage between any two of three classical three-dimensional species interaction systems—trrophic chain, competition, and polyphagy. It is shown that omnivory may be either stabilizing or destabilizing, depending, in part, on the conditions of the parent systems from which it derives. It is further conjectured that the tritrophic to competition gradient cannot be entirely stable, that there must be an instability at some level of intermediate omnivory.

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Although sometimes thought rare in nature, omnivory (consumption at more than one trophic level—sometimes referred to as intraguild predation), has recently been documented as a common phenomenon in a variety of ecosystems (Strong, 1992; Polis and Strong, 1996; Winemiller, 1990; Hall and Raffaelli, 1991). Furthermore, experimental studies (Spiller and Schoener, 1994; Holyoak and Sachdev, 1998; Arim and Marquet, 2004; Perfecto et al., 2004) as well as casual observations (e.g., small vertebrates such as birds and lizards are voracious consumers of both spiders and herbivorous insects), suggest that the phenomenon is important in nature, and even experimentally conclude that it is “stabilizing” (Fagan, 1997). This empirical reality might initially seem strange in light of an extensive earlier theoretical literature suggesting that the phenomenon would likely be destabilizing in the context of food webs (Pimm and Lawton, 1978; Pimm, 1982; Pimm et al., 1993; Emmerson and Yearsley, 2004).

In response to this notion of omnivory as a destabilizing force, some theoretical literature emphasized the idea that intrapopulational structure (including “life history omnivory”) is likely necessary to fully stabilize an omnivorous connection (Pimm and Rice, 1987; Mylius et al., 2001). However, much of that earlier literature was based on traditional Lotka–Volterra-like models and standard point set stability analysis in which the extra connection implied by omnivory indeed does tend to destabilize otherwise stable systems. However, more recent literature suggests that the omnivory connection may be stabilizing for more realistic modeling approaches (McCann and Yodzis, 1997) and/or more realistic notions of stability (Law and Blackford, 1992). The purpose of the present study is to cast the problem of omnivory in a general framework and, demonstrate that omnivory can be either stabilizing or destabilizing, depending on background conditions.

Elementary considerations of omnivory encounter three qualitatively distinct underlying structures, all emanating from classic three-dimensional systems. An omnivory connection to any of these three structures results in the same topology, as illustrated in Fig. 1. Omnivory is thus seen as the topological connection

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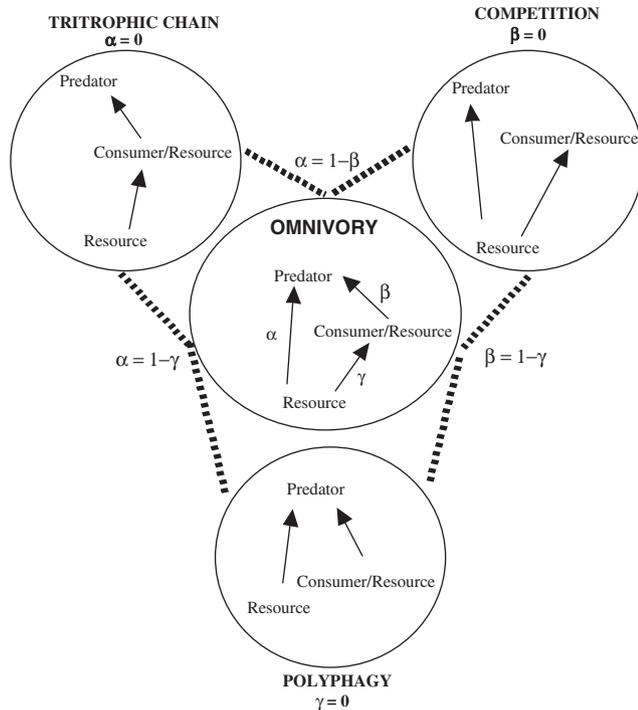


Fig. 1. Diagrammatic representation of the three possible gradients in which classic three-dimensional situations are united through the concept of omnivory. Parameters α , β and γ refer to the various positions of the parameter c in governing equations for each of the three gradients, as stated below each of the models in the text.

between three distinct three-dimensional forms—competition, polyphagy and the tritrophic chain. Furthermore, it is not difficult to cite particular circumstances that correspond to each of the three transformations (between competition and polyphagy, between competition and tritrophic and between polyphagy and tritrophic). For example, the recent work of Perfecto and colleagues (2004) established birds as predators on both spiders and herbivorous insects, but spiders were also predators on the herbivores. Thus, the question as to whether spiders represented mainly bird food (the system thus corresponding to a tritrophic) or alternative predators on the herbivores (the system thus corresponding to competition between birds and spiders) was effectively a question about the relative importance of omnivory in the system, along with the competition/tritrophic gradient (i.e., setting $\alpha = 1 - \beta$ in Fig. 1).

In formulating the basic question of omnivory it seems initially obvious to ask the simple question, is omnivory stabilizing or non-stabilizing, as has been done so frequently in the past. However, this simple question is not sufficiently refined for systematic study of the phenomenon. There are two issues that need to be addressed in refining the question. First, what is the meaning of stability and second, how is omnivory manifest.

Regarding the meaning of stability, the debate on this question is not likely to be resolved soon. The Lyapunov-like point set stability, in which a single point or cycle is automatically approached by a slight perturbation of the trajectory, as pioneered by early theoreticians (Lewontin, 1969) is clearly not what most ecologists have in mind when they speak of stability. Rather, the tendency to persist is a more likely metric of what is usually meant in talk of stability of ecosystems. In this work, stability will be taken to mean long-term persistence of a system, in accord with recent work on the subject (Law and Blackford, 1992; Kirlinger, 1986; Hofbauer and Sigmund, 1998). Other notions of persistence, for example, ability to recover after a disturbance, are of interest also, but not the focus of the present work.

The particular way in which omnivory is manifest is also not well defined by the simple question. For example, with reference to Fig. 1, in the tritrophic case, the predator may become an omnivore simply by increasing its consumption of the resource. However, it matters greatly whether that increase is relative to its consumption of the consumer/resource or the consumption of the resource by the consumer/resource. In one case the tritrophic structure gradually transforms toward a competition structure (if $\alpha = 1 - \beta$), in the other case it gradually transforms toward a polyphagy structure (if $\alpha = 1 - \gamma$). Casting omnivory as a point in the gradient between two basic three-dimensional cases was pioneered by McCann and Yodzis (1997), who explicitly studied part of the gradient from tritrophic to competition (Fig. 1). Note that my use of the term omnivory includes only those cases in which the consumer consumes a resource also consumed by one of its own food items, what might be referred to as “closed-loop” omnivory.

In this paper I systematically study the three gradients of omnivory, specifically asking the question whether omnivory tends to be stabilizing or destabilizing. The vehicle for studying this question is the construction of a parameter, c , which varies from 0 to 1.0, and which enters the equations differently for each of the three gradients studied, but acts as a constant reference point to study each system from one extreme to the other. However, since this parameter enters the equations differently depending on the biological construct under study, it has no fixed biological meaning. In each of the three cases it simply is a convenient way of causing the equations to smoothly transform from one extreme to the other. Using this device, the basic questions relating omnivory to stability can be asked generally for all three gradients (Fig. 1). Specifically, first, if one of the base-line structures (either tritrophic, competition or polyphagy) is inherently unstable, can omnivory act to stabilize it and second, if the base-line structure is unstable, can omnivory act to destabilize it? A related

query is whether omnivory is a phenomenon that permits a smooth and continuous transformation from one state to another (e.g., is it possible to go from polyphagy to competition without a loss of stability at some intermediate state of omnivory). As will be shown, such a smooth transformation is possible for the polyphagy/competition and polyphagy/tritrophic transformation, but conjecturally impossible for the tritrophic/competition transformation. Evidence for the latter conjecture is presented in the form of extensive numerical study, however, formal proof is elusive thus far.

1. Theory

The base-line cases have all been investigated thoroughly in the literature. The polyphagy case is probably the most well-known due to its relative tractability (Gilpin, 1979; Schaffer, 1985; Vandermeer, 1991). Substantial theoretical work has also been done on the tri-trophic system (Hastings and Powell, 1991; Yodzis and Innes, 1992; Klebanoff and Hastings, 1994; McCann and Yodzis, 1995; De Feo and Rinaldi, 1997). The three-dimensional competitive system, by conventional theory (i.e. Gause’s rule) cannot be stable (persistent), but with oscillations, stability is easily attained (Armstrong and McGehee, 1976, 1980; Huisman and Weissing, 2001; Abrams and Holt, 2002).

1.1. The tritrophic/competition gradient

As illustrated in Fig. 1, the tritrophic/competition gradient is defined by the predator gradually changing its eating habits from eating mainly the consumer/resource to eating mainly the resource. Natural situations corresponding to this situation are easy to see, qualitatively. For example, birds may concentrate on spiders (a tritrophic chain) or on the prey of spiders (and thus be competitors with them). In McCann and Hastings’ treatment of this case, the omnivory parameter was varied from 0 to 0.5 in order to examine the effect of omnivory on the tritrophic structure (with reference to Fig. 1, they studied $0 < \alpha < 0.5$). Here I extend the results of McCann and Hastings to the other extreme of resource competition. The results for $0 < \alpha < 0.5$ are, of course, identical to those of McCann and Yodzis (1997).

The following model incorporates both base forms where the parameter c has been substituted for α :

$$\dot{x}_1 = x_1 \left[r \left(1 - \frac{x_1}{K} \right) - \frac{a_1 x_2}{\theta_1} - \frac{c a_3 x_3}{\theta_2} \right], \tag{1a}$$

$$\dot{x}_2 = x_2 \left[\frac{a_1 x_1}{\theta_1} - \frac{(1-c)a_2 x_3}{\theta_2} - d_1 \right], \tag{1b}$$

$$\dot{x}_3 = x_3 \left[\frac{(1-c)a_2 x_2 + c a_3 x_1}{\theta_2} - d_2 \right], \tag{1c}$$

$$\theta_1 = 1 + b_1 x_1, \tag{1d}$$

$$\theta_2 = 1 + b_2 [(1-c)x_2 + c x_1], \tag{1e}$$

where x_i are the three state variables, r is the intrinsic rate of increase of x_1 , K is the carrying capacity of x_1 , a_i are the consumption constants, d_i are the death rates, θ_i are the functional response terms, and b_i are the parameters of the functional response. The parameter c is the “omnivory” parameter and varies between 0 (trophic chain—Fig. 1) and 1.0 (competition—Fig. 1). With $c = 0$ the system reverts to precisely the system studied by Hastings and Powell (1991) and with $c = 1$ the system reverts to precisely the system studied by Armstrong and McGehee (1976, 1980). With reference to Fig. 1, $\alpha = c$ and $\beta = 1 - c$.

First set parameters as follows: $r = 2$; $K = 3$; $a_1 = 8$; $a_2 = 0.05$; $a_3 = 0.6$; $d_1 = 0.1$; $d_2 = 0.01$; $b_1 = 5.5$; $b_2 = 0.4$. With this parameter set both the trophic chain formation ($c = 0$) and the consumer competition formation ($c = 1$) are persistent, both forming a simple limit cycle (Fig. 2a). However, adding non-zero values of c to the system rapidly destabilizes it, in the sense that x_2 rapidly drops out of the system (Fig. 2a). Thus, the traditional interpretation of omnivory as a destabilizing force is obtained with this particular formation. It should also be added that it is not difficult to invent cases in which x_3 is the component that is eliminated from the system by omnivory, or cases in which x_1 is first eliminated, followed by the elimination of the other two. Furthermore, setting the tritrophic system in chaos (the teacup attractor) does not change the outcome. The

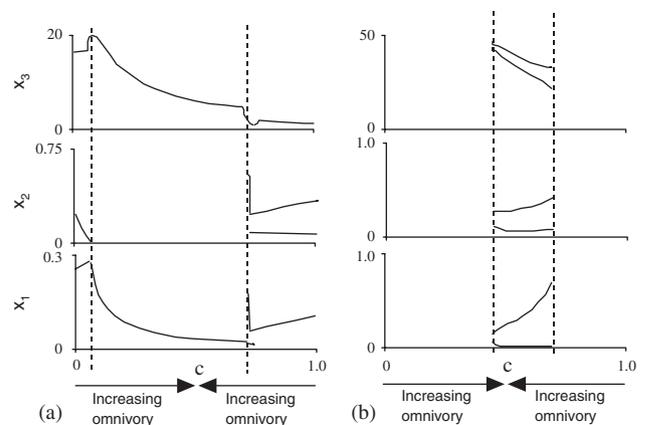


Fig. 2. Local maxima and minima as a function of degree of omnivory over the gradient of tritrophic ($c = 0$) to competition ($c = 1$): (a) instability caused by increasing omnivory, manifest in the extinction of x_2 from the system, dashed lines enclose the region of instability; (b) stability caused by increasing omnivory, dashed lines enclose the region of stability. See text for parameter values. Numerical solutions were obtained with a fourth degree Runge–Kutta routine here and in all other simulations.

general conclusion is that if we begin with a stable tritrophic situation ($c = 0$) and a stable competition situation ($c = 1$), where all the other parameters are the same for both tritrophic and competition, adding omnivory seems to destabilize the system, in that one or more components are eliminated through omnivory. This does not mean that weak omnivory cannot be sustained near either end of the spectrum. In a later Section I return to the idea that instability seems to be a general condition of omnivory if both ends of the continuum are stable.

However, another point of view is also possible, which was the point of [McCann and Yodzis \(1997\)](#) in their original formulation. We now set parameters as follows: $r = 2$; $K = 3$; $a_1 = 0.9$; $a_2 = 0.002$; $a_3 = 0.1$; $d_1 = 0.0001$; $d_2 = 0.0035$; $b_1 = 5.5$; $b_2 = 0.4$. With this parameter set both the trophic chain ($c = 0$) and competition ($c = 1$) are not persistent (indeed, x_1 is eliminated from the system in both cases, which leaves x_2 and x_3 with nothing to eat and thus they too are eliminated). However, with a range of intermediate values of c , the system is persistent with a limit cycle ([Fig. 2b](#)). Thus, beginning with two systems that are unstable with no omnivory (either $c = 0$ or $c = 1$), by adding omnivory, the system can be made to persist. The general conclusion is that if we begin with a three-dimensional system that is unstable in either its tritrophic configuration (as noted by [McCann and Yodzis, 1997](#)) or its competition configuration, the addition of omnivory to the system is able to stabilize it. A similar result was obtained for a chemostat model ([Kuijper et al., 2003](#)), and a resource-based model (where the x_1 variable is not autoreproductive) ([Mylius et al., 2001](#)) although these authors did not investigate parameters that would have given stability at both extremes. In both cases ([Kuijper et al., 2003](#); [Mylius et al., 2001](#)), the qualitative results of instability at the ends of the c spectrum with stability at intermediate values, can be deduced from the bifurcation diagrams they present.

1.2. The polyphagy/competition gradient

As illustrated in [Fig. 1](#), the polyphagy/competition gradient is defined by the predator gradually changing its eating habits from eating mainly the consumer/resource to eating mainly the resource. Natural situations corresponding to this situation are easy to see, qualitatively. For example, it is well known that many fish populations can become laden with stunted individuals ([Ylikarjula et al., 1999](#); [Schneider and Lockwood, 1997](#)). If those populations are piscivores that normally are competitors with other piscivores, their reduction in average size may shift their basic trophic position to one in which they convert to insectivores or small prey fish species which they avoided previously. Thus, a system in which the two piscivores were

competitive changes into a system in which the larger piscivore preys on the stunted population and the alternative smaller species—a change from competition to polyphagy in the scheme of [Fig. 1](#). This was effectively the rationale for introducing walleyed pike into Michigan lakes to attempt a reversal of the stunting of bluegills ([Schneider and Lockwood, 1997](#)).

The equations corresponding to this gradient are:

$$\dot{x}_1 = x_1 \left[r \left(1 - \frac{x_1}{K} \right) - \frac{ca_1x_2}{\theta_1} - \frac{a_3x_3}{\theta_2} \right], \tag{2a}$$

$$\dot{x}_2 = x_2 \left[(1 - c)r(1 - x_2) - \frac{(1 - c)a_2x_3}{\theta_2} + \frac{ca_1x_1}{\theta_1} - cd_1 \right], \tag{2b}$$

$$\dot{x}_3 = x_3 \left[\frac{(1 - c)a_2x_2 + a_3x_1}{\theta_2} - d_2 \right], \tag{2c}$$

$$\theta_1 = 1 + b_1(x_1 + cx_2), \tag{2d}$$

$$\theta_2 = 1 + b_2[(1 - c)x_2 + x_1]. \tag{2e}$$

With reference to [Fig. 1](#), $\gamma = c$ and $\beta = 1 - c$. Set parameters as follows: $r = 1$; $K = 1$; $a_1 = 1$; $a_2 = 1$; $a_3 = 3$; $d_1 = 0.3$; $d_2 = 0.3$; $b_1 = 0.1$; $b_2 = 5.5$. With this parameter set both the polyphagy formation ($c = 0$) and the competition formation ($c = 1$) are persistent, polyphagy forming a stable focal point and competition forming a simple limit cycle ([Fig. 3a](#)). However, adding non-zero values of c destabilize it, in the sense that x_3 drops out of the system ([Fig. 3a](#)). Again the traditional interpretation of omnivory as a destabilizing force can be obtained with this particular formation.

Alternatively, set parameters as follows: $r = 1$; $K = 1$; $a_1 = 1$; $a_2 = 1$; $a_3 = 3$; $d_1 = 0.3$; $d_2 = 0.12$; $b_1 = 0.1$; $b_2 = 5.5$. With this parameter set both the polyphagy

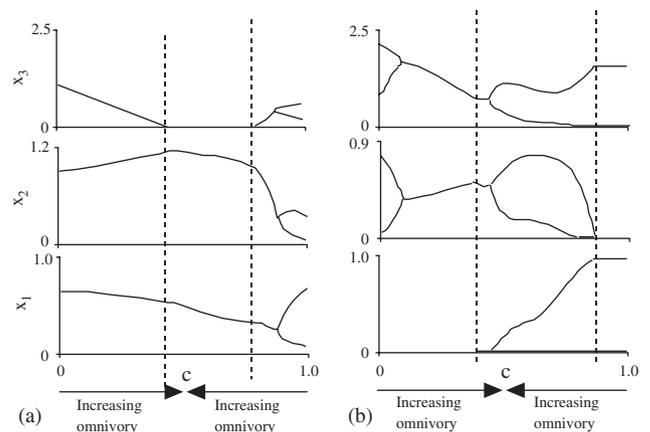


Fig. 3. Local maxima and minima as a function of degree of omnivory over the gradient of polyphagy ($c = 0$) to competition ($c = 1$): (a) instability caused by increasing omnivory, manifest in the extinction of x_3 from the system, dashed lines enclose the region of instability; (b) stability caused by increasing omnivory, dashed lines enclose the region of stability. See text for parameter values.

formation ($c = 0$) and the competition formation ($c = 1$) are unstable, x_1 eliminated from the polyphagy state and x_2 eliminated from the competition state (Fig. 3b). Adding non-zero values of c to the system rapidly stabilizes it. Again the alternative interpretation of omnivory as a stabilization force can be realized with this particular formation.

1.3. The tritrophic polyphagy gradient

As illustrated in Fig. 1, the polyphagy/tritrophic gradient is defined by the consumer/resource gradually changing its eating habits from eating mainly outside the system (implicitly modeled as the carrying capacity) to eating mainly the resource while at the same time the predator also switches from eating only the consumer/resource to also eating the resource. Natural situations corresponding to this situation are easy to see, qualitatively. For example, the manned wolf in south-eastern Brazil tends to eat reptiles and fruits in the dry months of the year and rodents and birds during the wet months (Silva and Talamoni, 2003). Since rodents and birds eat fruits also where reptiles generally do not, we see the possibility of a seasonal cycle involving the two ends of the trophic/polyphagy gradient, where predator = manned wolf, consumer/resource = reptiles in the dry season and birds/rodents in the wet season, and resource = plants (fruits).

The equations corresponding to this gradient are:

$$\dot{x}_1 = x_1 \left[r \left(1 - \frac{x_1}{K} \right) - \frac{ca_1x_2}{\theta_1} - \frac{(1-c)a_3x_3}{\theta_2} \right], \quad (3a)$$

$$\dot{x}_2 = x_2 \left[(1-c)r(1-x_2) - \frac{a_2x_3}{\theta_2} + \frac{ca_1x_1}{\theta_1} - cd_1 \right], \quad (3b)$$

$$\dot{x}_3 = x_3 \left[\frac{a_2x_2 + (1-c)a_3x_1}{\theta_2} - d_2 \right], \quad (3c)$$

$$\theta_1 = 1 + b_1x_1, \quad (3d)$$

$$\theta_2 = 1 + b_2[x_2 + (1-c)x_1]. \quad (3e)$$

With reference to Fig. 1, $\gamma = c$ and $\alpha = 1 - c$. Set parameters are as follows: $r = 1$; $K = 1$; $a_1 = 1$; $a_2 = 3$; $a_3 = 3$; $d_1 = 0.3$; $d_2 = 0.3$; $b_1 = 0.1$; $b_2 = 5.5$. In this case both polyphagy and tritrophic formations are stable, but the intermediate levels of omnivory generate instability, with the loss of x_2 (Fig. 4a).

Finally, set the parameters as: $r = 1$; $K = 1$; $a_1 = 1$; $a_2 = 2.5$; $a_3 = 2.3$; $d_1 = 0.3$; $d_2 = 0.3$; $b_1 = 0.1$; $b_2 = 5.5$. With this parameter set both the polyphagy ($c = 0$) and the tritrophic formation ($c = 1$) are unstable, but the intermediate levels of omnivory generate a broad range of persistence (Fig. 4b). As in the previous cases, the traditional interpretation of omnivory as a destabilizing force (Fig. 4a) can be obtained with this particular

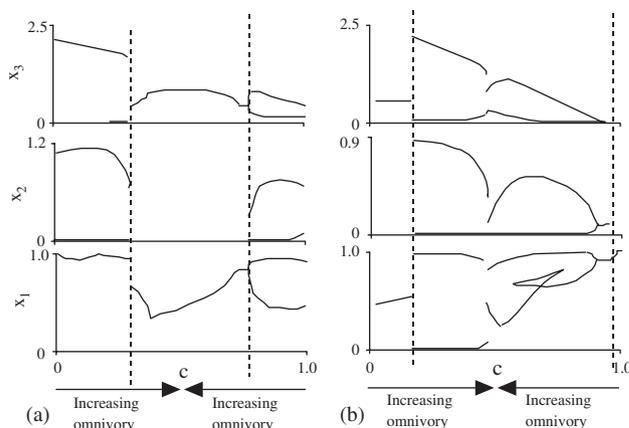


Fig. 4. Local maxima and minima as a function of degree of omnivory over the gradient of polyphagy ($c = 0$) to tritrophic ($c = 1$): (a) instability caused by increasing omnivory, manifest in the extinction of x_2 from the system, dashed lines enclose the region of instability; (b) stability caused by increasing omnivory, dashed lines enclose the region of stability. See text for parameter values.

formation, but with different parameter values omnivory can be stabilizing (Fig. 4b).

1.4. The smooth transition from base cases

An interesting theoretical question arises when considering the situation where both base conditions are stable. Is it possible that this stability will be maintained over the entire range of omnivory? Or is it somehow inevitable that the two extremes of stability will be interrupted with an unstable situation at some intermediate omnivory level (Figs. 2a, 3a, and 4a)? For two of the three basic gradients, it is not difficult to generate examples of smooth transitions from one state to another (Fig. 5). For the polyphagy to competition gradient set parameter values at: $r = 1$; $K = 1$; $a_1 = 1$; $a_2 = 1.7$; $a_3 = 3$; $d_1 = 0.3$; $d_2 = 0.3$; $b_1 = 0.1$; $b_2 = 5.5$, and the result is a smooth transition from a limit cycle at one end of the gradient to a limit cycle at the other end, interrupted by a stable focal point (Fig. 5a). For the polyphagy to tritrophic gradient set parameters at $r = 1$; $K = 1$; $a_1 = 1$; $a_2 = 3$; $a_3 = 1.6$; $d_1 = 0.3$; $d_2 = 0.3$; $b_1 = 0.1$; $b_2 = 5.5$, and the result is a continuous limit cycle over the entire omnivory gradient (Fig. 5b).

In the case of the tritrophic to competition gradient in which both ends of the continuum are stable, it does not seem possible to invent a parameter combination in which the system is stable for all values of c . Thus in moving from a mainly tritrophic chain to a mainly consumer resource competition, one or more of the components will be lost in some intervening state. So, for example, in a terrestrial ecosystem in which vertebrate predators (e.g., lizards, birds) mainly eat spiders and spiders eat herbivorous insects (e.g., Spiller and Schoener, 1994), if the vertebrates switch from

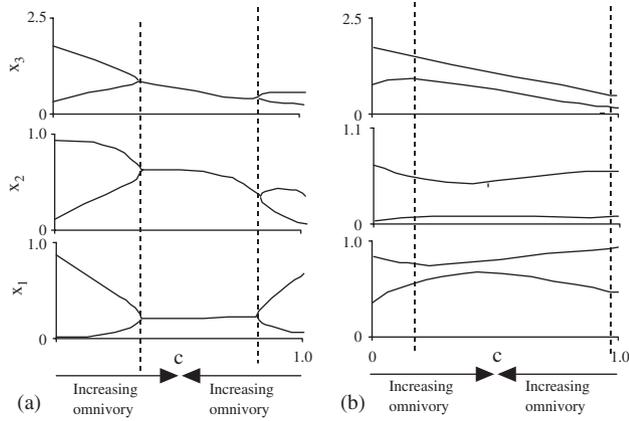


Fig. 5. Local maxima and minima as a function of degree of omnivory over the gradient of polyphagy ($c = 0$) to tritrophic ($c = 1$): (a) the competition to polyphagy transition, dashed lines enclose the region of a stable focal point; (b) the polyphagy to tritrophic transition. See text for parameter values.

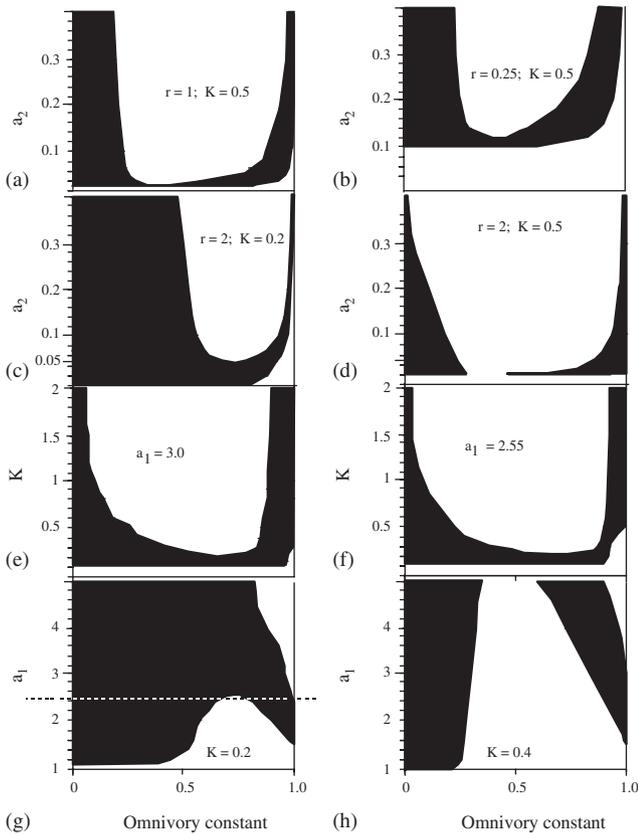


Fig. 6. Parameter space studies for the tritrophic chain to competition gradient. Shading indicates permanence of all three species; non-shading indicates extinction of one or more species. Unless indicated otherwise, parameters are $r = 2$; $a_1 = 8$; $a_2 = 0.05$; $a_3 = 0.6$; $d_1 = 0.1$; $d_2 = 0.01$; $b_1 = 5.5$; $b_2 = 0.4$, and the abscissa is always the range of omnivory from $c = 0$ to 1.0: (a, b) changing r from 1 to 0.25, (c, d) changing K from 0.2 to 0.5, (e, f) changing a_1 from 3.0 to 2.5, (g, h) changing K from 0.2 to 0.4.

spiders to herbivores during the season, during the time of switch, the system clearly is expected to go through a bottleneck in which long term persistence is impossible.

While a proof of this conjecture is at this point elusive, an extensive search for an example of a continuous transformation without an intervening extinction has failed. In Fig. 6 eight illustrative parameter spaces are shown (many other sections of parameter space were examined) with shading indicating presence of all three species and no shading indicating extinction of one or more of the species. A smooth transition without extinction thus would occur if it were possible to draw a straight horizontal line at any point in these parameter spaces such that the line did not intersect a non-shaded area. In several cases, it is possible to draw such a line in which there is only a very small amount of intervening non-shaded area (e.g., the dotted line in Fig. 6(g)). However, an extensive search revealed only cases in which the stability was always interrupted by an extinction at intermediate values of omnivory.

It is necessary to emphasize that the non-existence of a parameter set in which the tritrophic/competition gradient is stable for all values of c is, at this point, only a conjecture. After extensive simulations with many parameter sets, searching for such a state, it seems to be the case that it is impossible. However, this conjecture awaits formal proof.

2. Discussion

Both ends of the continuum, in all three formulations (Fig. 1), can be arranged such that they are stable, in the sense of all three components persisting in perpetuity. Whether the parameter values required to set these initial conditions are reasonable from a biological point of view is not of interest here, since my purpose is to demonstrate potential existence. It is almost certain that for some parameter ranges in real systems it will not be possible to reproduce the complete range of results presented in Figs. 2–5. However, it is useful to know that fixed conclusions about the stabilizing or destabilizing nature of omnivory cannot be made based on the structure of the food web alone, which can be done through numerical study, demonstrating counterexamples to each purported generalization. That has been the intent of this contribution.

The parameter c in all three sets of equations has been construed as a weighting parameter, allowing a smooth transition from one extreme to another. Whenever $0 < c < 1$, omnivory occurs. However, the exact nature of the omnivory depends on the parent systems from which it derives. A biological interpretation of the parameter c can be invented for each case, but such an exercise is not of particular interest for the present study. Rather, it should be interpreted only as the relative amount of omnivory, in the context of which of the three continua is being studied.

Armstrong and McGehee (1976) referred to the “bandwidth” of coexistence to refer to the range of parameter values within which two species could coexist, a concept employed by Abrams and Holt (2002) in their detailed study of predator–prey oscillations. Such a concept could be applied here as well, but would clearly have to be done in the context of particular types of food webs under consideration. A system of vertebrate predators, insect herbivores, and plants would have a considerably different spectrum of possible parameter universes than a system of hyperparasitoid, parasitoid, and insect, which would be different from a virus, bacteriophage, and bacteria. Clearly, future studies of such parameter spaces with regard to the stabilizing potential of omnivory would be of great interest.

It is clear that in each formulation, the two ends of the continuum are united by the concept of omnivory (Fig. 1). Using this conceptualization it is possible to enter the long-standing debate about the nature of omnivory as a stabilizing or destabilizing force. Indeed, setting the two ends of the continuum so as to be stable, omnivory can be destabilizing in that intermediate positions on the continuum between the tritrophic and the strong competition may be unstable (Figs. 2a, 3a, and 4a). Thus, omnivory is destabilizing. On the other hand, it is also possible to invent situations in which both extremes are unstable but intermediate positions are stable (Figs. 2b, 3b, and 4b). Thus omnivory is stabilizing. I conclude that the consequence of omnivory depends on the stability conditions of the parent systems from which it derives.

Note that the examples presented herein are intended to make the point that omnivory can be either stabilizing or destabilizing, depending on the context. It should not, however, be somehow construed that when both ends of one of the continuum are unstable, omnivory will stabilize the system and when both ends are stable, omnivory will destabilize them. It is elementary to construct examples where omnivory has no effect at all on stability.

An especially interesting case is shown in Fig. 5a in which the stability changes from limit cycles at both endpoints to stable focus for intermediate values of the parameter c , suggesting a double set of Hopf bifurcations along the omnivory gradient. In other words, the real parts of the eigenvalues of the Jacobian matrix must be negative at some intermediate values of c and must pass through 0 with non-zero slope as c approaches both 0 and 1.0. It has not been possible to verify this conjecture analytically, although the basic structure of the bifurcation diagram strongly implies that it must be true.

Formulating the problem of omnivory in this way suggests questions of evolutionary interpretation. As noted elsewhere (Diehl and Feiße, 2000), there will frequently be an evolutionary advantage to omnivory.

However, the various ways in which omnivory can arise create a complicated mosaic for making generalizations. If we consider only the tritrophic to competition scenario, it is reasonable to ask whether the predator gains an advantage from becoming an omnivore, which could occur through two distinct pathways—from the competitive situation, if the predator begins to eat the consumer/resource or from the tritrophic situation, if the predator begins to eat the resource. Questions of evolutionary change thus focus on the predator. Yet if there is reason to suspect that from the tritrophic situation the predator will always gain from increasing its omnivorous habit, the unstable nature of this particular transformation will ultimately limit such an evolutionary trajectory.

Contrarily, if we analyse either the polyphagy/tritrophic or the polyphagy/competition transformation, evolutionary speculations are less obvious. Thus, for example, the process of developing omnivory along the polyphagy/tritrophic gradient involves not a change in eating habits, but a change in susceptibility of the resource to consumption by either the predator or consumer/resource. Such changes are likely to depend far more on the specific biological characteristics of both resource and consumer/resource, than on the phenomenon of omnivory itself.

Of more direct interest are cases in which changes along one of the transformational gradients occur in ecological time. The case of the seasonally variable eating habits of the manded wolf has already been mentioned ((Silva and Talamoni, 2003). A more complicated situation is reported for the western flower thrips (Agrawal et al., 1999) in which the predator is the thrips, *Frankliniella occidentalis*, which eats both herbivorous mites and the plants on which they feed. In the relative absence of mites the thrips eat mainly plants, but when mites begin feeding on the plant, the plant generates an induced cue that causes the thrips to feed less on the plant, switching its feeding preference to the mites. Thus, plant-induced defenses have the tendency to move the system from competition base line to the tritrophic baseline, thus maintaining the omnivorous habit of the thrips. This is the situation in which an intermediate level of omnivory tends to be destabilizing, suggesting that the induced defenses of the plant may in the end be a destabilizing force when taken as part of the food web as a whole.

In the context of larger webs, omnivorous connections are extremely common (Polis, 1991; Polis and Strong, 1996; Winemiller, 1990; Hall and Rafaelli, 1991; but see Williams and Martinez, 2004). Their overall effects may be stabilizing or destabilizing, depending on the structure of the web, and no generalizations seem possible at the present time. However, from the extremely simple webs presented herein, there is little doubt that omnivory can be either stabilizing or

destabilizing, depending on the base line consideration on which the comparison is made.

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References

- Abrams, P.A., Holt, R.D., 2002. The impact of consumer–resource cycles on the coexistence of competing consumers. *Theor. Popul. Biol.* 62, 281–295.
- Agrawal, A.A., Kobayashi, C., Thaler, J.S., 1999. Influence of prey availability and induced host–plant resistance on omnivory by western flower thrips. *Ecology* 80, 518–523.
- Arim, M., Marquet, P.A., 2004. Intraguild predation: a widespread interaction related to species biology. *Ecol. Lett.* 7, 557–564.
- Armstrong, R.A., McGehee, R., 1976. Coexistence of species competing for shared resources. *Theor. Popul. Biol.* 9, 317–328.
- Armstrong, R.A., McGehee, R., 1980. Competitive exclusion. *Am. Nat.* 115, 151–170.
- De Feo, O., Rinaldi, S., 1997. Yield and dynamics of tritrophic food chains. *Am. Nat.* 150, 328–345.
- Diehl, S., Feiße, M., 2000. Effects of enrichment on three-level food chains with omnivory. *Am. Nat.* 155, 200–218.
- Emmerson, M., Yearsley, J.M., 2004. Weak interactions, omnivory and emergent food-web properties. *Proc. R. Soc. London Ser. B* 271, 397–405.
- Fagan, W.F., 1997. Omnivory as a stabilizing feature of natural communities. *Am. Nat.* 150, 554–567.
- Gilpin, M.E., 1979. Spiral chaos in a predator–prey model. *Am. Nat.* 107, 306–308.
- Hall, S.J., Rafaelli, D., 1991. Food-web patterns: lessons from a species rich web. *J. Anim. Ecol.* 60, 823–842.
- Hastings, A., Powell, T., 1991. Chaos in a three species food chain. *Ecology* 72, 896–903.
- Hofbauer, J., Sigmund, K., 1998. *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge.
- Holyoak, M., Sachdev, S., 1998. Omnivory and the stability of simple food webs. *Oecologia* 117, 413–419.
- Huisman, J., Weissing, F.J., 2001. Biological conditions for oscillations and chaos generated by multispecies competition. *Ecology* 82, 2682–2695.
- Kirlinger, G., 1986. Permanence in Lotka–Volterra equations: linked predator–prey systems. *Math. Biosci.* 82, 165–191.
- Klebanoff, A., Hastings, A., 1994. Chaos in three-species food chains. *J. Math. Biol.* 32, 427–451.
- Kuijper, L.D.J., Kooi, B.W., Zonneveld, C., Kooijman, S.A.L.M., 2003. Omnivory and food web dynamics. *Ecol. Model.* 163, 19–32.
- Law, R., Blackford, J.C., 1992. Self-assembling food webs: a global viewpoint of coexistence of species in Lotka–Volterra communities. *Ecology* 73, 567–578.
- Lewontin, R.C., 1969. The meaning of stability. In: *Diversity and Stability in Ecological Systems*. Brookhaven Symposia in Biology, number 22.
- McCann, K., Yodzis, P., 1995. Bifurcation structure of three-species food chain model. *Theor. Popul. Biol.* 48, 93–125.
- McCann, K., Yodzis, P., 1997. Re-evaluating the omnivory–stability relationship in food webs. *Proc. R. Soc. London B* 264, 1249–1254.
- Mylius, S.D., Klumpers, K., de Roos, A.M., Persson, L., 2001. Impact of intraguild predation and stage structure on communities along a productive gradient. *Am. Nat.* 158, 259–276.
- Perfecto, I., Vandermeer, J.H., López Bautista, G., Ibarra Nuñez, G., Greenberg, R., Bichier, P., Langridge, S., 2004. Greater predation in shaded coffee farms: the role of resident neotropical birds. *Ecology* 85 (10), 2677–2681.
- Pimm, S.L., 1982. *Food Webs*. Chapman & Hall, New York.
- Pimm, S.L., Lawton, J.H., 1978. On feeding on more than one trophic level. *Nature (London)* 275, 542–544.
- Pimm, S.L., Rice, J.A., 1987. The dynamics of multispecies, multi-life-stage models of aquatic food webs. *Theor. Popul. Biol.* 32, 303–325.
- Pimm, S.L., Lawton, J.H., Cohen, J.E., 1993. Food web patterns and their consequences. *Nature (London)* 350, 669–674.
- Polis, S.L., 1991. complex trophic interactions in deserts: an empirical critique of food-web theory. *Am. Nat.* 138, 123–155.
- Polis, G.A., Strong, D.R., 1996. Food web complexity and community dynamics. *Am. Nat.* 147, 813–846.
- Schaffer, W.M., 1985. Order and chaos in ecological systems. *Ecology* 66, 93–106.
- Schneider, J.C., Lockwood, R.N., 1997. Experimental management of stunted bluegill lakes. Fisheries Research Report 2040, Michigan Department of Natural Resources, Ann Arbor.
- Silva, J.A., Ta. amoni, S.A., 2003. Diet adjustments of maned wolves, *Chrysocyon brachyurus* (Illiger) (Mammalia, Canidae), subjected to supplemental feeding in a private natural reserve, Southeastern Brazil. *Rev. Bras. Zool.* 20, 339–345.
- Spiller, D.A., Schoener, T.W., 1994. Effects of top and intermediate predators in a terrestrial food web. *Ecology* 75, 182–196.
- Strong, D.R., 1992. Are trophic cascades all wet? Differentiation and donor control in species ecosystems. *Ecology* 73, 747–754.
- 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.
- Williams, R.J., Martinez, N.D., 2004. Limits to trophic levels and omnivory in complex food webs: theory and data. *Am. Nat.* 163, E458–E468.
- Winemiller, K.O., 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* 60, 331–367.
- Ylikarjula, J., Heino, M., Dieckman, U., 1999. Ecology and adaptation of stunted growth in fish. *Evol. Ecol.* 13, 433–453.
- Yodzis, P., Innes, S., 1992. Body size and consumer–resource dynamics. *Am. Nat.* 139, 1151–1175.