

# Enrichment and Foodchain Stability: The impact of different forms of predator-prey interaction

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## Abstract

We propose a simple model of an ecological foodchain of arbitrary length. The model is very general in nature and describes a whole class of foodchains. Using the methods of qualitative analysis the model's stability can be analyzed without restricting the predator-prey interaction to any specific functional form. The model can therefore be used to study the effect of different functional forms on the stability of the foodchain. We demonstrate that the stability of steady states may strongly depend on the exact functional form of the interaction function used. It is shown that a class of interaction functions exists, which are similar to the widely used Holling functions but bestow radically different stability properties upon the model. An example is shown in which enrichment has a stabilizing effect on the foodchain. By contrast enrichment destabilizes steady states if Holling functions are used.

*Key words:* Ecosystem stability, Bifurcation, Dynamics, Foodchain, Enrichment

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## 1 Introduction

Since the pioneering work of Lotka (1925) and Volterra (1926) many models of ecological foodchains have been proposed (s. for instance DeAngelis (1992)). Foodchain models with constant parameters are often found to approach a steady state in which the species coexist in equilibrium. However, if parameters are changed, sudden, discontinuous transitions to other types of dynamical behavior may occur. The critical parameter values at which such transitions happen are called bifurcation points. Typical examples of bifurcations are

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the Hopf bifurcation (Hopf 1942) which corresponds to the transition from stationary to oscillatory behavior or the transcritical bifurcation in which two steady states meet and exchange their stability.

Bifurcations can be expected to exist in almost all foodchain models (s. for instance Edwards and Brindley (1996), Gragnani et al. (1998), Boer et al. (1998), Busenberg et al. (1990)). From an ecological point of view bifurcations endanger the existence of particular species in the foodchain. A stable steady state that undergoes a bifurcation will in general either lose its stability or disappear entirely. Beyond the bifurcation, the system will approach some other attractor on which the long-term dynamics will be either stationary, periodic, quasiperiodic or chaotic. Even if the foodchain ends up in another steady state the transition to that state will often involve the extinction of one or more levels of the foodchain. On the other hand the entire foodchain may survive in a non-stationary state, but further bifurcations may be encountered which ultimately lead to local extinction of species.

In order to preserve the system under consideration in its natural state, crossing bifurcations should be avoided. Since anthropogenic influences can not be prevented altogether, it is of great importance to determine the critical parameter values at which bifurcations occur. Knowing these, the risk induced by disturbing the system can be assessed. Bifurcations have been computed for many specific models of different complexity. In ecosystem modeling complex models are often required to describe a given natural system realistically. However, in order to understand the general mechanisms leading to bifurcations in ecosystems, much simpler, conceptual models are needed.

Given the importance of understanding foodchain dynamics it is not surprising that many conceptual foodchain models have been proposed (DeAngelis 1992). All of these are specific in the sense that a specific functional form of predator-prey interaction is assumed. In foodchain models Holling-type functions are used most frequently. As we will see in the following, these functions satisfy some basic biological requirements and have the advantage of mathematical simplicity. However, there is no biological reason to prefer these functions over others of similar shape.

The investigation of specific models has revealed that there are some features which almost all simple foodchain models share. However, we have to check whether these features can be observed in nature or appear due to common simplifications. For instance, it was first realized by Rosenzweig (1971) that increasing the supply of nutrients or prey tends to destabilize steady states in simple foodchain models. This "Paradox of Enrichment" is widely believed to occur in most simple models. However, in nature the Paradox of Enrichment has rarely been verified (Sommer 1984, Ebenhöf 1988, Morin and Lawler 1995). The destabilizing effect of enrichment has been observed in some exper-

iments (Luckinbill 1974, Tilman and Wedin 1991). However, in other systems enrichment had no effect (McCauley and Murdoch 1990) or stabilized food-chain dynamics (Kirk 1998, McCauley et al. 1999).

In this paper we demonstrate that the exact functional form of the interaction function or predator functional response is of importance. This function describes the interaction between foodchain levels. So far general interaction functions have been considered in terms of persistence and global stability (Gard 1980, Freedman and So 1985). Although global stability insures the survival of species, it is a very strong requirement that can only be met by few realistic foodchains. The weaker notion of persistence likewise guarantees survival of species, but not necessarily in the natural state. By contrast, we follow the approach of Saunders and Bazin (1974) and focus on local stability which is much more important for actual applications. Furthermore we propose a simple method for measuring the stabilizing or destabilizing effect of a given interaction function.

We start by formulating a general foodchain model in Sec. 2. The main advantage of the model is that its stability can be analyzed without having to specify the interaction functions in any way. The bifurcations in which the initial loss of steady state stability occurs are described in Sec. 3. We discuss some general results of the bifurcation analysis in Sec. 4. Most importantly we find that the effect of interaction functions can be measured in terms of a parameter  $\Gamma$  that depends on the exact functional form of predator-prey interactions. We compute  $\Gamma$  for some interaction functions in Sec. 5. The calculations reveal that all commonly used functions (i.e. Holling functions) behave in a similar way. If these functions are used a steady state can never be stabilized by enrichment. However, other predator-prey interaction functions exist which lead to different stability properties. In this case moderate enrichment may stabilize steady states. In Sec. 6 we present sufficient conditions for the occurrence of such behavior. These conditions show that many reasonable interaction functions exist which bestow unusual stability properties upon the model. An intuitive picture is presented which allows to determine  $\Gamma$  directly from the plot of the interaction function. We summarize our results in Sec. 7.

## 2 A General Foodchain Model

In this section we formulate a conceptual foodchain model. The aim of this model is to describe a general foodchain with as few parameters as possible. General, easily interpretable parameters are preferred over specific ones for which interpretation can be complicated.

We consider a foodchain consisting of  $N$  active trophic levels. Depending on

the system under consideration a level of the foodchain may describe one species or a functional group of similar species. Likewise, we use  $X_n$  to denote the biomass density or the abundance in level  $n$ . The species on level  $n$  are assumed to prey solely on species on the immediately lower level  $n - 1$ . Furthermore we assume that the biomass loss due to predation in level  $n - 1$  is proportional to  $X_n$  while it is some function  $G_{n-1}$  of  $X_{n-1}$ . Only a fraction  $\eta_n$  of the biomass flow is converted to predator biomass. Taking these factors into account we obtain a set of  $N$  ordinary differential equations (ODEs)

$$\dot{X}_n = \eta_n G_{n-1}(X_{n-1})X_n - G_n(X_n)X_{n+1} \quad n = 1 \dots N. \quad (1)$$

In these equations two additional variables  $X_0$  and  $X_{N+1}$  appear. The abundance of the nutrient  $X_0$  should be given in terms of an algebraic equation, which we assume to depend only on  $X_1$ . By doing so we assume that the dynamics of the nutrient is sufficiently fast. However, this restriction could be easily lifted by setting  $X_0 = 1$  and considering  $X_1$  as the nutrient.

The variable  $X_{N+1}$  may be interpreted as the abundance of a super predator. In reality the super predator may be an actual predator of even higher trophic level. Likewise, it may be used to describe any other cause of biomass loss in the top predator population, like natural mortality, disease or cannibalism. We do not model the super predator dynamics explicitly but assume that it inflicts a linear mortality (linear closure) on the top predator

$$G_N(X_N)X_{N+1} \sim X_N \quad (2)$$

Our model contains  $N$  interaction functions  $G_0 \dots G_{N-1}$  also known as predator response functions. We will not restrict these functions to any specific functional form, but demand that  $G_0 \dots G_{N-1}$  are smooth and

$$G_n(X_n) > 0 \quad \forall X_n > 0, n = 0 \dots N. \quad (3)$$

In this case the model has at least one positive steady state. Without choosing any specific functional form for  $G_0 \dots G_{N-1}$  explicit calculation of the steady state abundances  $X_1^*, \dots, X_N^*$  is impossible. We can however use our knowledge of the existence of the steady state to normalize the system.

We define the normalized abundances by

$$x_n := \frac{X_n}{X_n^*} \quad n = 1 \dots N. \quad (4)$$

The normalized steady state is

$$x_1^* = \dots = x_N^* = 1. \quad (5)$$

Furthermore we define normalized interaction functions

$$g_n(x_n) := \frac{G_n(X_n)}{G_n(X_n^*)} = \frac{G_n(X_n^* x_n)}{G_n(X_n^*)} \quad n = 0 \dots N - 1. \quad (6)$$

Note that

$$g_n(x_n^*) = 1. \quad (7)$$

Defining the constants

$$\alpha_n := \eta_n G_{n-1}(X_{n-1}^*), \quad (8)$$

$$\beta_n := \frac{X_{n+1}^*}{X_n^*} G_n(X_n^*) \quad (9)$$

we may write Eqs. (1) as

$$\dot{x}_n = \alpha_n g_{n-1}(x_{n-1}) x_n - \beta_n g_n(x_n) x_{n+1} \quad n = 1 \dots N. \quad (10)$$

If the system is in the steady state, Eq. (10) can be simplified to

$$\alpha_n = \beta_n, \quad n = 1 \dots N. \quad (11)$$

Since  $\alpha_n$  and  $\beta_n$  are constants this relation has to hold even if the system is not in the steady state. We may write Eq. (10) as

$$\dot{x}_n = \alpha_n (g_{n-1}(x_{n-1}) x_n - g_n(x_n) x_{n+1}) \quad n = 1 \dots N. \quad (12)$$

Finally, we can use time normalization to obtain  $\alpha_1 = 1$ .

So far we have used mathematical techniques to simplify the model. Let us now compute the system's Jacobian before considering further simplification based on biological reasoning. The Jacobian  $J$  is an  $N \times N$  matrix which determines the behavior of the model close to the steady state (see for instance Argyris et al. (1994), Glendinning (1994), Ott (1997), Kuznetsov (1995), Guckenheimer and Holmes (2002)). It is defined by

$$J_{ij} := \left. \frac{\partial \dot{x}_i}{\partial x_j} \right|_{\vec{x}=\vec{x}^*}. \quad (13)$$

In the normalized steady state the Jacobian of our model system may be written entirely in terms of  $\alpha_1 \dots \alpha_N$  and the parameters

$$\gamma_n := \left. \frac{\partial}{\partial x_n} g_n(x_n) \right|_{\vec{x}=\vec{x}^*}, \quad n = 1 \dots N. \quad (14)$$

$$h := - \left. \frac{\partial}{\partial x_1} g_0(x_0(x_1)) \right|_{\vec{x}=\vec{x}^*}. \quad (15)$$

We obtain

$$\mathbf{J} = \begin{pmatrix} \alpha_1 & & & & & \\ & \alpha_2 & & & & \\ & & \ddots & & & \\ & & & \alpha_{N-1} & & \\ & & & & \alpha_N & \end{pmatrix} \begin{pmatrix} (1 - \gamma_1 - h) & -1 & & & & \\ & \gamma_1 & (1 - \gamma_2) & -1 & & \\ & & \ddots & \ddots & \ddots & \\ & & & & \gamma_{N-2} & (1 - \gamma_{N-1}) & -1 \\ & & & & & \gamma_{N-1} & 0 \end{pmatrix}$$

In order to compare foodchains of different length it is desirable to make the number of parameters independent of the length of the foodchain. We achieve this by making two more assumptions. First, an allometric slowing-down is observed in most foodchains (Moloney and Field 1989). That is, the dynamics on every level of the foodchain is  $r$ -times as fast as the dynamics on the immediately lower level. We model this quite universal behavior by assuming

$$\alpha_n = r^{n-1} \quad n = 1 \dots N, \quad (16)$$

with  $0 < r \leq 1$ .

In the given normalization interactions between similar species should produce similar values of  $\gamma$ . Therefore the values of  $\gamma_1 \dots \gamma_{N-1}$  may be assumed to be identical. We define

$$\Gamma := \gamma_1 = \dots = \gamma_{N-1} \quad (17)$$

Equation (17) is clearly the strongest one of our assumptions. However, this assumption is only needed to avoid having too many parameters, which would make the presentation of the results difficult. Our conclusions will not depend strongly on this assumption. In the general case we would have different  $\gamma_1 \dots \gamma_{N-1}$ . The analysis outlined below can be applied to each of these individually.

Using the assumptions made above general foodchains of arbitrary length can be studied in terms of the parameters  $r, h$  and  $\Gamma$ , which can be interpreted as follows: The parameter  $r$  describes the dependence of the timescale on the trophic level. If  $r = 1$  the dynamics on each trophic level takes place on the same timescale, while smaller values of  $r$  slows predator dynamics down. The parameter  $\Gamma$  indicates the predators sensitivity to prey abundance. If  $\Gamma$  is high predators react very sensitive to a decline in prey population. Finally,  $h$  describes the sensitivity of the primary producer  $X_1$  to the amount of available nutrients  $X_0$ . In systems with high carrying capacity  $h$  will generally be small while in systems with low carrying capacity  $h$  is close to one.

### 3 The Steady State's Loss of Stability

Having derived a simple expression for the general Jacobian we may now start to analyze the stability of the normalized steady state. A steady state is stable if all eigenvalues of the system's Jacobian (computed in the steady state) have negative real parts. The eigenvalues depend smoothly on the parameters of the system under investigation. If parameters are changed a loss of stability occurs if the real parts of one or more eigenvalues become positive.

We can distinguish two different ways in which eigenvalues may acquire positive real parts. In the first case a single real eigenvalue crosses the imaginary axis. This corresponds in general to a saddle-node bifurcation. Because of certain symmetries this bifurcation is in foodchains often encountered in form of a transcritical bifurcation. Saddle-node bifurcations may be seen as collisions of steady states. In case of the transcritical bifurcation both steady states survive the collision but exchange their stability properties. From the ecological point of view a transcritical bifurcation is merely a transition from one steady state to another. Therefore a transcritical bifurcation will not endanger species survival unless a state in which species are extinct is directly involved. In this paper we include the computation of saddle-node bifurcations for the sake of completeness. However, from the ecological point-of-view another bifurcation, the Hopf bifurcation, is of far greater importance.

In a Hopf bifurcation (Hopf 1942) a pair of complex conjugate eigenvalues of the Jacobian crosses the imaginary axis. While the steady state becomes unstable a stable limit cycle emerges (supercritical Hopf bifurcation) or an unstable limit cycle vanishes (subcritical Hopf bifurcation). In either case the Hopf bifurcation marks the transition from stationary to oscillatory behavior. In case of a subcritical Hopf bifurcation the oscillations are transient and persist only until the system approaches some other attractor. After the supercritical Hopf bifurcation the system will approach the stable limit cycle on which the whole system may survive in an oscillatory state. However, as

parameters are varied further, subsequent bifurcations which destroy the limit cycle's stability are likely to occur.

In our simple foodchain model extinction of species can not occur (cf. Eq. (3)). However, the model is well suited to analyze the primary loss of stability of the steady state. The point in which this loss of stability occurs (and the system's natural mode of existence breaks down) will in general be a Hopf bifurcation.

So far we have identified the bifurcations by their characteristic eigenvalue constellations. Unfortunately, exact computation of the eigenvalues is only possible for very small systems. For larger systems one would usually resort to numerical techniques. However, using one of the standard software packages for numerical bifurcation analysis has some disadvantages. Although most software works well with a large number of parameters the specific functional form of the system has to be known. We will instead follow an analytical approach that allows us to deduce the bifurcations from the Jacobian alone. Since we can not compute the eigenvalues of the Jacobian analytically, test-functions have to be constructed. A test-function is an implicit function that has the bifurcation as a unique solution. Demanding the determinant of the Jacobian to vanish yields a test-function for saddle-node and transcritical bifurcations. Since the eigenvalues behave in the same way in both bifurcations we can not distinguish them with the chosen degree of generality. For Hopf bifurcations a suitable analytical test-function can be constructed using the method of resultants (Guckenheimer et al. 1997). As mentioned above, the Hopf bifurcation may be sub- or supercritical. We can not distinguish between these two cases based on the test-function. In order to decide whether the sub- or the supercritical case has been encountered, one would have to compute normal forms which would require additional knowledge about the form of the interaction functions. From the test-functions, the actual bifurcations can be computed using computer algebra systems. For a detailed presentation of the method we refer to (Gross and Feudel 2003), since the derivations are rather lengthy and beyond the scope of this paper.

## 4 Bifurcations of General Foodchains

After having discussed the bifurcations and their detection in general, we can now proceed with the analysis of the foodchain model. We will present the results of this analysis in form of three-parameter bifurcation diagrams. Since this method of presentation is rather uncommon and may confuse the reader at first we will start by discussing the fairly simple case of the di-trophic (two level) foodchain before moving on to longer foodchains.

The bifurcation diagram for the di-trophic foodchain is shown in Fig. 1. The



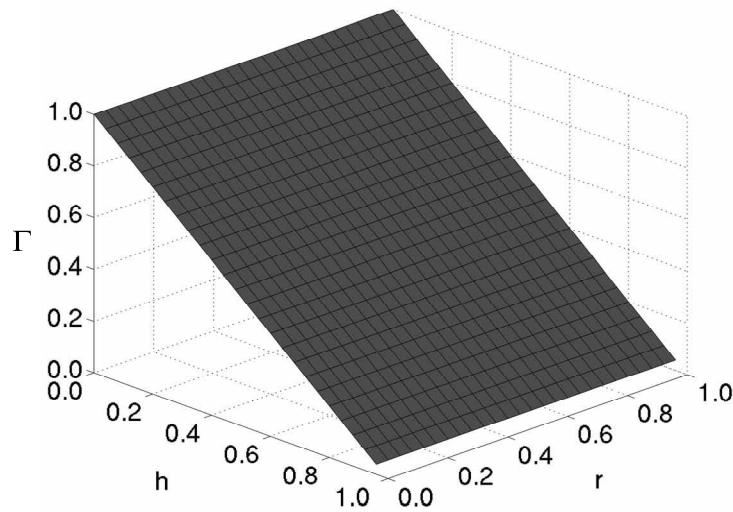


Fig. 1. Bifurcation diagram of the di-trophic foodchain with linear closure. The Hopf bifurcation (grey surface) divides areas of qualitatively different dynamics. The steady state is stable above the surface.

three axes of the diagram are spanned by the three parameters  $r$ ,  $h$  and  $\Gamma$ . Every point in the three dimensional space of the diagram corresponds to a foodchain with specific parameter values. Most of these foodchains exhibit qualitatively similar dynamics, whereas foodchains with qualitatively different dynamics are separated by bifurcations.

In case of the di-trophic foodchain there is only one bifurcation affecting the stability of the steady state. This is a Hopf bifurcation which is shown in the diagram as a grey surface. The bifurcation surface divides the parameter space into two volumes. All parameter combinations found in the top volume correspond to foodchains in which the normalized steady state is stable. If we move through the diagram by varying parameter values, the steady state will remain stable until the Hopf bifurcation surface is crossed. It will then become unstable and will remain so in the entire lower volume. Since the stability of the steady state is lost, the system will now approach some other attractor. This new attractor will probably be a limit cycle. However the exact nature and the bifurcations of this attractor can not be determined with the chosen degree of generality.

Let us now study the bifurcations of the tri-trophic (three level) foodchain. The bifurcation diagram is shown in Fig. 2. In addition to the Hopf bifurcation (grey surface) there is a saddle-node bifurcation shown in white. This bifurcation will in general be a transcritical bifurcation. In the following transcritical (saddle-node) bifurcations will always be shown in white while all grey surfaces correspond to Hopf bifurcations. The space of the bifurcation diagram is

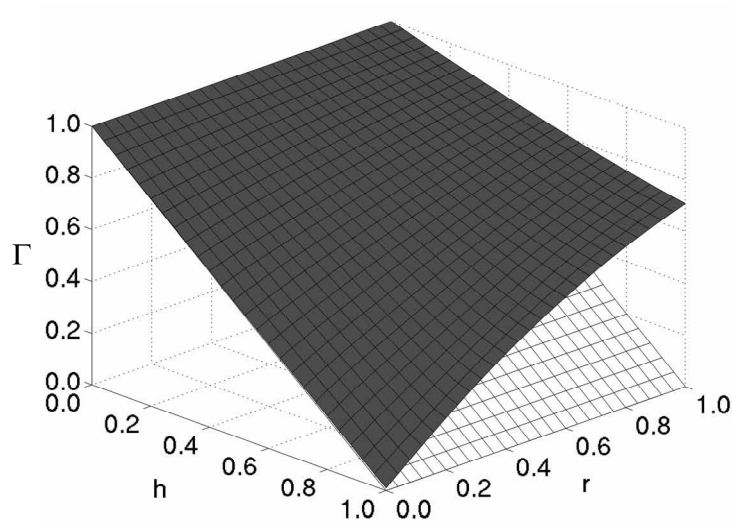


Fig. 2. Bifurcation diagram of the tri-trophic foodchain. Apart from Hopf bifurcation (grey surface) a transcritical bifurcation (white surface) has been found.

now divided into three volumes. Again, the normalized steady state is stable above the Hopf bifurcation surface and unstable everywhere else.

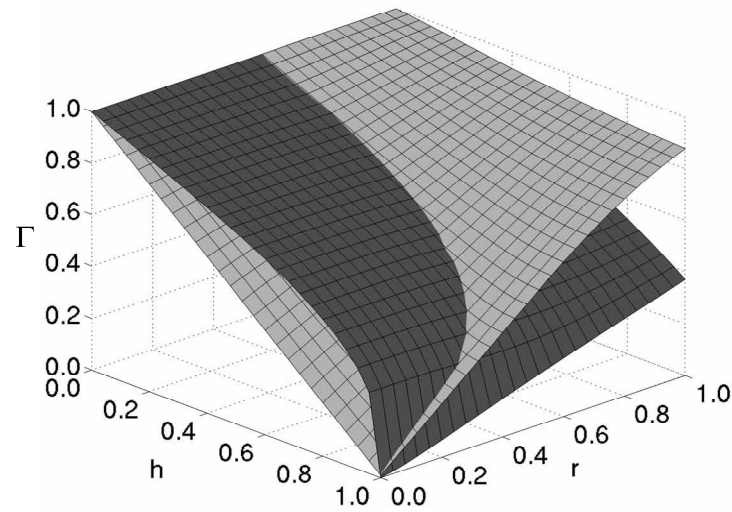


Fig. 3. Bifurcation diagram of the four-trophic foodchain. The steady state stability is lost by crossing one of the two Hopf bifurcation surfaces.

Since the transcritical bifurcation separates two volumes in which the steady state is unstable it is not significant for our stability analysis. However, the presence of the bifurcation proves that there has to be more than one steady state. This is a result of surprising generality given the fact that we have not decided on any specific form of  $g_0 \dots g_{N-1}$ . Since we have normalized a general

steady state our bifurcation diagrams are valid for all steady states individually. Note however, that the parameters in the bifurcation diagram depend on the normalization and therefore on the steady state under consideration.

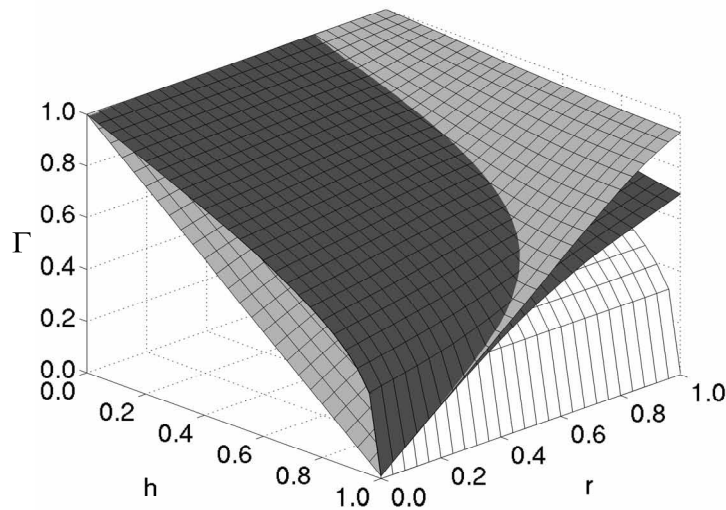


Fig. 4. Bifurcation diagram of the five-trophic foodchain. Apart from the two Hopf bifurcations (grey surfaces) a transcritical bifurcation (white surface) has been found.

The bifurcation diagrams of foodchains of length four to six are shown in Fig. 3-5. These diagrams contain even more bifurcation surfaces. In fact, the number of Hopf bifurcations equals the foodchain length divided by two (rounded down). A transcritical bifurcation is present in all foodchains of odd length. Like in the case of shorter foodchains, the normalized steady state is only stable above all surfaces.

In any case the steady state can be stabilized by making the predators sufficiently sensitive to prey density (high  $\Gamma$ ). Likewise, high values of  $h$  (which will usually occur in oligotrophic systems) have a stabilizing effect. However, unlike  $\Gamma = 1$  setting  $h = 1$  is not always sufficient to stabilize the steady state. The stabilizing effect of  $h$  is more pronounced if  $r$  is small, that is if separation of predator and prey timescales is large. Generally, similar timescales ( $r \approx 1$ ) lead to instability.

## 5 Functional Forms of Predator-Prey Interaction

In the previous section we have shown that high  $\Gamma$  is always beneficial. This is reasonable since high  $\Gamma$  indicates that the predators are very sensitive to the abundance of their prey. The stabilizing effect of increased sensitivity to

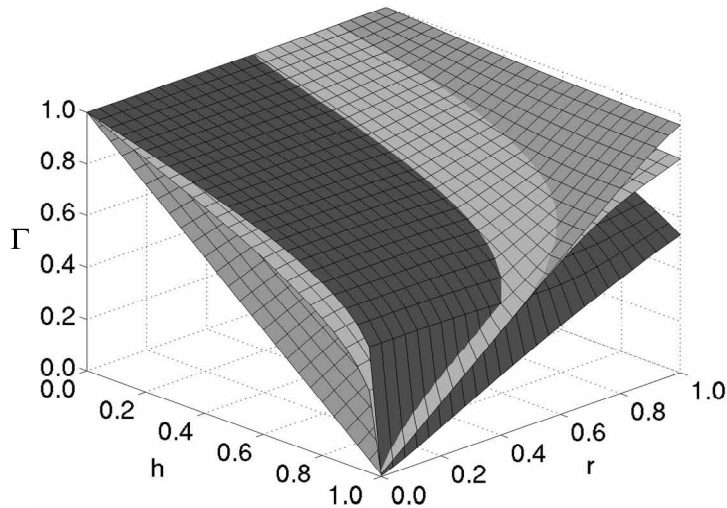


Fig. 5. The bifurcation diagram of the six-trophic foodchain contains three Hopf bifurcation surfaces.

prey density is very general and can be expected to be found in almost all ecosystems. For instance Saunders and Bazin derive a condition that guarantees stability of a steady state in a simple chemostat model (see Eq. (32) in Saunders and Bazin (1974)). This condition may be written as  $\Gamma > 1$  in our context. It is therefore reasonable to use  $\Gamma$  to measure the *interactive stability*, that is the stability of the predator-prey interaction induced by the predator's sensitivity to prey density.

In this section we investigate the effect of enrichment on the interactive stability. In the classical enrichment scenario the ecosystem is enriched by increasing the nutrient supply. In our context this would increase the parameter  $h$  and decrease the parameters  $\gamma_1, \dots, \gamma_{N-1}$  by different amounts depending on the form of the interaction. In order to obtain results for general interactions we will study an abstract form of enrichment. In this simplified scenario  $h$  stays constant while  $\Gamma$  decreases. Although it is a simplification to consider only the effect of changes in  $\Gamma$ , essentially the same analysis could be applied to the parameter  $h$  and the parameters  $\gamma_1, \dots, \gamma_{N-1}$  individually. The investigation of more realistic scenarios is therefore likely to yield very similar but less general results.

In the following the index  $n$  will be dropped for the sake of simplicity. We start by considering the well-known Holling-function of type II

$$G(X) = \frac{AX}{K + X}, \tag{18}$$

where  $A$  is the maximum predation rate and  $K$  is the half saturation constant. The function rises linearly if  $X$  is small. At larger values of  $X$  the slope of the function decreases as the predator becomes saturated.

By applying Eq. (6) and introducing the dimensionless parameter

$$\chi := \frac{X^*}{K} \tag{19}$$

we obtain

$$g(x) = \frac{(1 + \chi)x}{1 + \chi x}. \tag{20}$$

Using the definition of  $\Gamma$  we get a monotonously decreasing function

$$\Gamma = \frac{1}{1 + \chi}. \tag{21}$$

The value of the parameter  $\chi$  may be seen as an indicator of prey density. If prey is abundant,  $\chi$  will be large. For  $\chi \rightarrow \infty$  we get  $\Gamma \approx 0$  and the steady state is unstable. By contrast, an ecosystem in which prey is scarce has  $\chi \approx 0$ . This results in  $\Gamma \approx 1$  and high interactive stability.

In case of the Holling type II function it is not surprising that decreasing  $\chi$  moves the steady state into an area in which the function  $g(x)$  rises faster and consequently  $\Gamma$  is higher. The Holling type II function is based on the assumption that predation rate is proportional to prey density if prey is scarce. However, if the predator actively seeks out large concentrations of prey the Holling type III function

$$G(X) = \frac{AX^2}{K^2 + X^2} \tag{22}$$

is more appropriate. Since the slope of this function goes to zero for small values of  $X$  it may be suspected that the foodchain will be destabilized if prey concentration gets too small. However, this is not the case.

Let us consider the general Holling function

$$G(X) = \frac{AX^\alpha}{K^\alpha + X^\alpha}. \tag{23}$$

Function	$G(X)$	$\Gamma(\chi)$
Lotka-Volterra	$AX$	1
General Holling	$\frac{AX^\alpha}{K^\alpha + X^\alpha}$	$\frac{\alpha}{1 + \chi^\alpha}$
Multiple Saturation	$AX^M \prod_{m=1}^M (K_m + X)^{-1}$	$\sum_{m=1}^M (\chi_m + 1)^{-1}$
Gamov	$A \exp(-K/X)$	$1/\chi$
Ivlev	$A(1 - \exp(-X/K))$	$1 + \frac{(\chi+1) \exp(-\chi)}{1 - \exp(-\chi)}$
Power law	$AX^\alpha$	$\frac{1}{\alpha}$

Fig. 6. Some interaction functions  $G(X)$  and the corresponding stability functions  $\Gamma(\chi)$ . ( $\chi := X^*/K$ ,  $\chi_m := X^*/K_m$ )

Normalization yields

$$g(x) = \frac{(1 + \chi^\alpha)x^\alpha}{1 + \chi^\alpha x^\alpha} \quad (24)$$

and therefore

$$\Gamma = \frac{\alpha}{1 + \chi^\alpha}. \quad (25)$$

For  $\alpha > 0$  Eq. (25) is similar to Eq. (21). Abundant prey destabilizes the foodchain while scarce prey is always stabilizing. The half-saturation point  $\chi = 1$  is also the point where  $\Gamma$  reaches its half maximal value. The highest possible value of  $\Gamma$  is  $\alpha$  which is reached as  $\chi \rightarrow 0$ .

The values of  $\Gamma(\chi)$  for some other interaction functions are shown in Fig. 6. The commonly used interaction functions produce similar behaved functions for  $\Gamma(\chi)$ . However, some of the other functions show slightly different behavior. For instance the interaction function proposed by Ivlev (1961) yields a monotonously decreasing function for  $\Gamma(\chi)$ . Like Holling foodchains, Ivlev foodchains will be destabilized by enrichment. However, for the Ivlev function, the interactive stability  $\Gamma$  will remain greater than one. Therefore enrichment can not destabilize Ivlev foodchains sufficiently far to cause bifurcations. If power functions are used to model the interaction,  $\Gamma$  will not depend on  $\chi$  at all. Enrichment will therefore have neither stabilizing nor destabilizing effect.

Interaction functions like the power functions or Ivlev's function are generally regarded as less realistic than for instance Holling functions. We may ask ourselves if realistic functions could exist, which have qualitatively different stability properties. To answer this question let us first specify what is meant by *realistic*.

A realistic interaction function should be based on biological hypotheses. Common interaction functions like the Lotka-Volterra function or the Holling functions can be derived from very basic assumptions. As more and more facts about the system are taken into account, more detailed hypotheses can be formulated and more complex interaction functions can be derived. Since it is often unclear which details of the interactions are important a large number of possible interaction functions may be derived.

However, in order to be realistic all possible interaction functions should share some common properties. They should for instance not allow the predator to grow arbitrarily fast, even if prey is abundant. Furthermore, the shape of the function for low prey densities can often be guessed. In the intermediate region, between very low and very high prey densities, the interaction function can in most cases be expected to be increasing.

Apart from these basic biological considerations there is in general few experimental evidence that would allow us to prefer one specific interaction function over others of similar shape. Especially in the interesting intermediate region the predator-prey interaction may depend on all sorts of details, like for instance adaption. In this sense the Holling functions are by far not the only *realistic* interaction functions, but merely the simplest of realistic approximations.

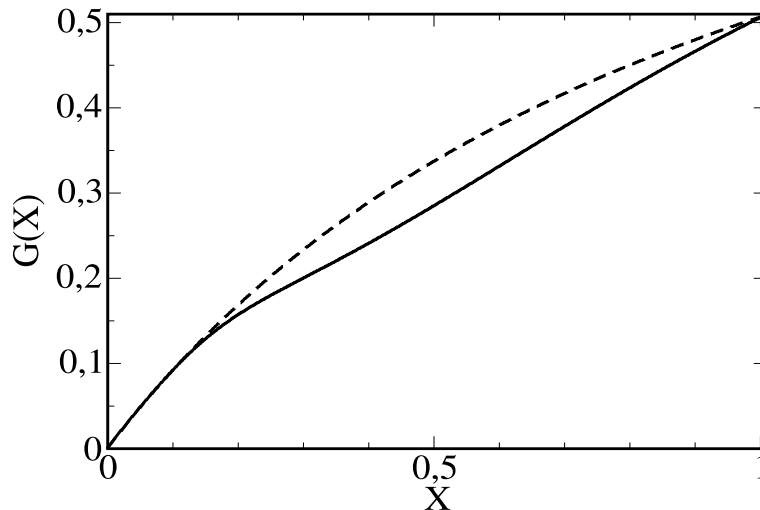


Fig. 7. The proposed interaction function (Eq. 26) in comparison with a Holling type II function (dashed) for  $K = 1$ . It is hard to decide which function is better suited to describe predator-prey interaction in any given system.

In the light of our inability to determine the *true* interaction function, it has to be checked if the choice of one specific function will effect the predictions of the model in a qualitative way.

Consider for instance

$$\begin{aligned}
 G(X) &= \frac{2V(X) + 2^{U(X)/V(X)}U(X)}{2 + 2^{U(X)/V(X)}}, \\
 U(X) &= \frac{X}{X + K}, \\
 V(X) &= \frac{X^2}{X^2 + K^2}.
 \end{aligned}
 \tag{26}$$

This functions is realistic in the sense described above. In fact, it can be derived from the hypothesis that the individual predators are able to choose between two predation strategies which are described by Holling type II and Holling type III respectively. As a result the function is quite similar to the Holling type II function (see Fig. 7). Since Eq. (26) lacks the mathematical simplicity of the Holling type II, the corresponding equation for  $\Gamma$  is rather lengthy. The stability functions corresponding to the Holling type II function and the proposed function Eq. (26) have been plotted in Fig. 8. The plot reveals that, although the interaction functions  $G(X)$  are similar in shape the stability functions  $\Gamma(\chi)$  differ dramatically. For Eq. (26) we find a large interval in which  $\Gamma(\chi)$  increases with increasing  $\chi$ . In this interval enrichment has a stabilizing effect.

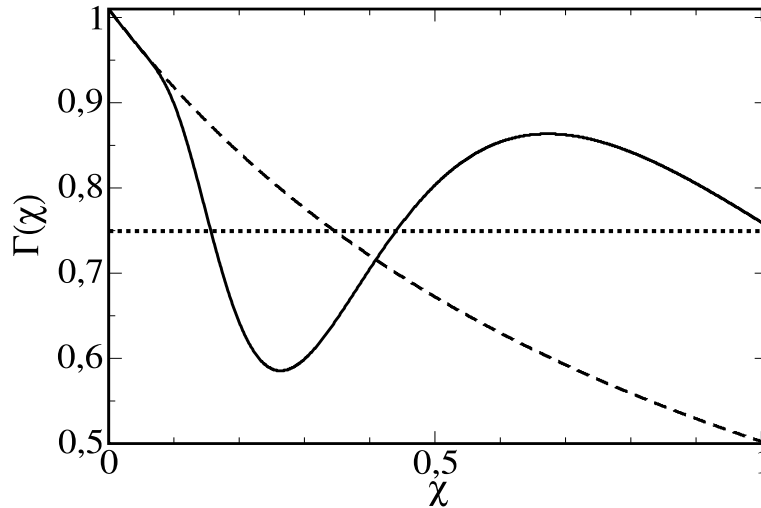


Fig. 8. Comparison of the stability functions corresponding to the proposed interaction function (Eq. 26) and Holling type II (dashed). The plot reveals the qualitative differences of the stability functions.

Let us illustrate our results by considering the di-trophic foodchain again. Suppose we have  $h = 0.25$ . From Fig. 1 it can be seen that in this case the stability of the steady state is lost by crossing the Hopf bifurcation at



$\Gamma = 0.75$ . This stability boundary appears in Fig. 8 as a horizontal line. The steady state is stable if  $\Gamma(\chi)$  is above the line. For the Holling type II function this is the case if  $\chi < 1/3$ . Beyond this point the steady state is unstable. For the interaction function Eq. (26) the steady state is stable for  $\chi < 0.16$  or  $0.44 < \chi < 1$ . Therefore increasing  $\chi$  from say 0.3 to 0.6 will result in a stabilization of the steady state.

In general, a system in which Eq. (26) has been used to model species interactions would have different stability properties than a model in which Holling functions have been used. Of course, we can not expect to find a real ecosystem in which the interaction of species follows Eq. (26) exactly. But on the other hand we can also not expect to find a real ecosystem in which the interaction function is exactly Holling type II.

The example of Eq. (26) shows that even minor changes in the shape of the interaction function can alter the stability function in a qualitative way. In the following section we show that this function is no special case, but only one example from a large class of functions. The implications of this important result will be discussed in Sec. 7.

## 6 The relationship between interactive stability and interaction function

In the previous section we have seen that there are interaction functions which are similar to commonly used functions but have different stability properties. In this section we go one step further and give some sufficient conditions for the existence of points of extremal stability. These conditions show that many biologically reasonable interaction functions exist which share this feature. As a byproduct we develop an intuitive understanding of the relationship between the shape of the interaction function  $G(X)$  and the interactive stability  $\Gamma$ .

We start by writing  $\Gamma(X^*)$  in the form

$$\Gamma(X^*) = \left( \frac{\partial G(X^*x)}{\partial x G(X^*)} \right)_{x=1} \quad (27)$$

$$= \frac{X^*}{G(X^*)} \left( \frac{\partial G(X)}{\partial X} \right)_{X=X^*}. \quad (28)$$

This expression may be simplified by defining

$$S(X^*) := \left. \frac{\partial G(X)}{\partial X} \right|_{X=X^*}, \quad (29)$$

$$R(X^*) := \frac{G(X^*)}{X^*}. \quad (30)$$

Note that  $S(X^*)$  is the slope of  $G(X)$  in  $X^*$  while  $R(X^*)$  is the average slope of  $G(X)$  in the interval  $[0, X^*]$ . Using  $R(X^*)$  and  $S(X^*)$  we may write the interactive stability as

$$\Gamma(X^*) := \frac{S(X^*)}{R(X^*)}. \quad (31)$$

The interactive stability may therefore be determined by measuring the position of the steady state, the value of  $G(X^*)$  and the slope of  $G(X)$  in the steady state. This can be advantageous if no mathematical expression for  $G(X)$  is available or the analytical computation presented in the previous section is too complicated.

Having obtained a more intuitive understanding of the interactive stability we can now ask ourselves for which interaction function points of extremal stability exist. We know that the interactive stability of biologically reasonable interaction functions is positive at  $X^* = 0$ , but approaches zero as  $X^*$  goes to infinity. We can therefore expect  $\Gamma(X^*)$  to be decreasing for high values of  $X^*$ . In order to show that a local maximum of stability exists it is therefore sufficient to prove that the interactive stability is increasing at some point.

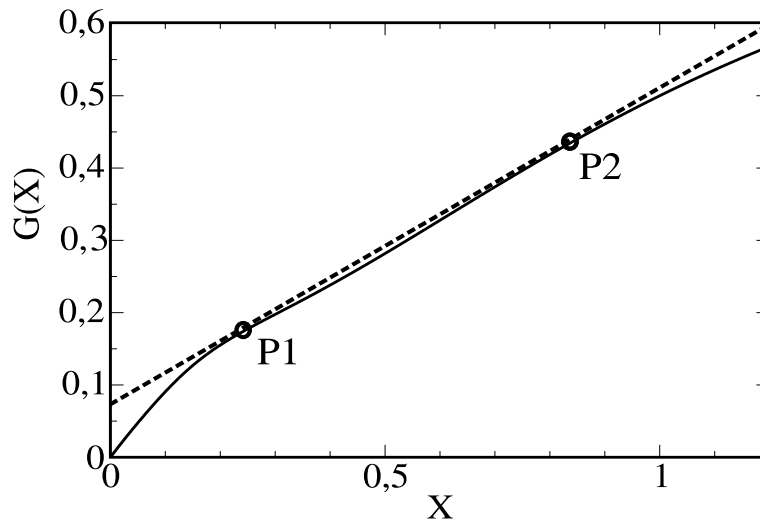


Fig. 9. Plot of the interaction function proposed in Eq. (26) (solid line). The existence of a common tangent of two points intersecting the positive y-axis (dashed line) proves that points of extremal stability have to exist.

Let us assume that two points  $X^*_1$  and  $X^*_2$  exist in which the interaction

function has the same slope. Because of Eq. (31) the interactive stability has to increase between  $X^*_1$  and  $X^*_2$  if  $R(X^*_1)$  is larger than  $R(X^*_2)$ . There is a very elegant way to show that this is the case in our example from Eq. (26). Figure 9 shows a plot of the interaction function. A line has been drawn which is the common tangent of two points of the interaction Function. The existence of this line proves that the slope in the two points is identical. The fact that the line intersects the y-axis at positive values shows that  $R$  decreases between the points. Therefore the existence of a common tangent which intersects the positive y-axis is a sufficient condition for the existence of a point of extremal stability.

In the light of the common tangent argument it is obvious that the example shown in the previous section is no special case. However, the existence of the common tangent is not always necessary. If  $R(X^*)$  decreases monotonously, as it does in the example, the existence of two points with the same slope alone is sufficient to prove the existence of points of extremal stability. On the other hand, if  $R(X^*)$  is not monotonous it will in general have extrema. It can be easily shown that a point of extremal stability has to exist between two neighboring extrema of  $R(X^*)$ .

The sufficient conditions presented here show that points of extremal interactive stability can appear in many reasonable interaction functions. They also show that minor modifications in the interaction functions can cause significant changes in the stability properties of the model. Models in which the predator can adapt to prey concentration (for instance by changing strategies) are especially likely to exhibit points of extremal stability. It is therefore not surprising that a strong paradox of enrichment has only rarely been observed in nature.

## 7 Conclusions

In this paper we have proposed a very general model for foodchains of arbitrary length. We have shown that the stability of steady states may be measured in terms of the interactive stability parameter  $\Gamma$ . We have then investigated how different functional forms of predator-prey interaction effect this parameter.

Our analysis revealed that all commonly used predator-prey interaction functions behave in a similar way. If these functions are used, enrichment will always have a destabilizing effect on the steady states of the foodchain.

However, the modeler should be aware that the stability properties depend strongly on the shape of the interaction function. Realistic interaction functions exist that are of similar shape as the standard functions (s. Fig. 6) but

correspond to qualitatively different stability properties. The example shown demonstrates that these interaction functions may for instance produce large intervals in parameter space in which enrichment stabilizes the foodchain. The sufficient conditions for the occurrence of points of extremal stability given in the previous section show that such points exist in many possible interaction functions.

In the light of our findings the absence of a strong paradox of enrichment in many natural foodchains is not surprising.

Our results suggest that the commonly used interaction functions may not describe the stability properties of many systems correctly.

The common interaction functions have been derived from simple biological hypotheses. They have the advantage of mathematical simplicity and describe the steady state abundances of many systems with reasonable accuracy. Nevertheless, more detailed biological hypotheses can be formulated which lead to more complex interaction functions. It seems reasonable to assume that minor details of the interaction between species will not effect the model in a qualitative way. However, we have shown that this is not always true. Even seemingly minor changes in the interaction function can cause qualitative changes in the stability of steady states.

This indicates that interaction functions in conceptual as well as in complex models should be chosen very carefully. It can be expected that the predictions of many models regarding stability may be improved by choosing interaction functions which differ from the commonly used ones.

It would be highly desirable to derive conditions which allow the modeler to decide which types of ecological details have to be taken into account to describe the stability properties of a given system realistically. In this paper we have given three sufficient conditions. Using these conditions one can confirm if certain modifications of the interaction function effect the models stability in a qualitative way. However, in order to rule out other possible modifications which have little or no effect on stability the derivation of necessary conditions is equally desirable.

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