

Invading species can stabilize simple trophic systems

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Abstract

Bifurcation analysis is presented for the dynamics of a nutrient–two-prey–predator bi-trophic food web in a chemostat. A simple model where food is converted into energy with a fixed efficiency is used. The available energy is used for maintenance and the rest for growth. The Holling type II functional response is used to model the ingestion rate of the prey consuming the nutrient as well as the predator consuming the two-prey species. The invasion of a competitor of the prey into a nutrient–prey–predator bi-trophic food chain is evaluated using bifurcation diagrams. We will show that an invading competitor prey can stabilize an oscillatory nutrient–prey–predator system. It is well known that in the absence of the predator generally one prey can invade and establish itself while the other is eliminated: this is called competitive exclusion. We will show that the presence of a predator can allow coexistence of two competing prey populations. This illustrates a top-down effect, where one species (predator) affects the interaction of two other species (competing prey). Bifurcation analysis results are here applied to community assembly theory; regions of invasibility were obtained using available computer packages based on the bifurcation theory with the implementation of continuation techniques. Regions with multiple interior attractors can be distinguished systematically. We discuss the applicability of the proposed technique for large-scale food webs. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

In the ecological community assembly approach species, newly generated species, (Post and Pimm, 1983), or species from a finite pool of potential colonists, (Drake, 1990) are added at random to an existing food web, starting with resources. The classical continuous-time Lotka–Volterra model, May (1973), is used and the

analysis is focused on equilibrium behavior. The main results are that communities become increasingly resistant to invasion (Post and Pimm, 1983; Drake, 1990), and that there can be more than one uninvadable state for a given species pool (Drake, 1990). Their criterion for invasion is completely based on the equilibrium values, which are rather easy to calculate for a Lotka–Volterra system. Law and Morton (1996) propose a technique based upon a global criterion for coexistence of species, known as permanence, introduced by Hofbauer and Sigmund (1988), which applies also when the community displays

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non-equilibrium dynamics. For a Lotka–Volterra system they derive a criterion using the equilibrium values where the density of the invader is zero. Invasion is possible when the initial rate of increase of the new species is positive. For a Lotka–Volterra system this holds true irrespective of whether the attractor of the virgin system is a fixed point or a periodic or chaotic orbit (Morton and Law, 1997).

The one-predator, two-competing prey model is an example of a (simple) ecological community model. A Lotka–Volterra model for this system is studied in a large number of papers (see for instance Klebanoff and Hastings, 1994). Kretzschmar et al. (1993) study a one-predator, two-prey model, where the functional response for the predator–prey interaction is Holling type II. The competition between the prey species is again described with a Lotka–Volterra competition model. Kretzschmar et al. (1993) describe a geometrical method for studying the different sets of conditions for permanence in biologically meaningful regions of the parameter space.

Modelling the growth of the prey species without the abiotic nutrient implies hidden assumptions about the availability of this nutrient. In the bioenergetic food web models discussed here, non-reproducing nutrients at the base are modelled explicitly. These models obey mass conservation laws. They can be formulated for various environmental conditions. Here, a continuous flow culture with constant influx of the nutrient and a constant dilution rate for all trophic levels, as in the chemostat, is assumed. The main subject of this paper is to analyze such a small-scale food web and to illustrate the consequences for the community assembly approach of a (hyperbolic) Holling type II instead of a (linear) Lotka–Volterra functional response, that is, consumption rate becomes saturated as nutrient density increases.

Smith and Waltman (1994) (pp. 14) study competition in the chemostat between microorganisms feeding on a common resource modelled explicitly. The Monod model is used for the growth of the species consuming the nutrients. The Monod model (Monod, 1942) is classical in the dynamics of populations consisting of unicellular microor-

ganisms. In that model the food ingestion rate is given by the Holling type II functional response. A fixed portion of the ingested food is used for growth. Gagnani and Rinaldi (1995) remark that: “this model can be considered a minimum model for plankton dynamics in eutrophic water bodies”. In an extension of this model a part of the assimilated energy is used for maintenance. This model is called the Marr–Pirt model (Pirt, 1965). It is equivalent to the model with different removal (depletion) rates of the populations discussed by Smith and Waltman (1994). They prove that coexistence is only possible when both species have exactly balanced parameters, a situation which cannot be expected to be found in nature. This phenomenon is called ‘competitive exclusion’. Which competitor survives in the culture vessel while the other is washed out, depends on the vital parameter values of both competitors. These conditions are derived by Smith and Waltman (1994) and they are reconsidered in this paper. Furthermore, a competitor predator (Fig. 1) is introduced by Smith and Waltman (1994) and it is proved that this can produce coexistence of the predator species only as an oscillatory phenomenon.

In previous articles Boer et al. (1998) and Kooi et al. (1998a) we studied a microbial tri-trophic nutrient–prey–predator–top-predator food chain (Fig. 1). Stable equilibria, periodic orbits but also complex, including chaotic, dynamic behavior can occur. In Kooi et al. (1999) we derived the invasion criterion for the invasion in a food chain. The Lyapunov exponent associated with the dynamics of the invader has to be positive on the exterior attractor.

Here we will explore invasion of a competing prey into the bi-trophic nutrient–prey–predator food chain. The problem is expressed in terms of dynamical system theory, especially bifurcation analysis, see for example Guckenheimer and Holmes (1985), Kuznetsov (1995) and Bazykin (1998). This approach was pioneered by Bazykin (1998), who analyzed and compared a great number of models of interacting populations. Detailed information on the asymptotic dynamical behavior of the system is obtained in this way. The emphasis is on the calculation of the bifurcation

points in the parameter space where the dynamics changes abruptly when a parameter is changed.

Transcritical bifurcations are most important for invasion. Two, generally equivalent, criteria can be derived for invasibility (Appendix A). The first criterion states that the necessary, and in general also sufficient, condition for invasion is that the invader's growth rate has to be larger than its depletion rate when rare. When the virgin nutrient–prey–predator food chain oscillates this has to hold for the average along the limit cycle for the invader's net growth rate. The second criterion, which holds true for most food webs where the rate of the change of the population biomass density is proportional to the biomass

density itself, uses an eigenvalue analysis. One eigenvalue of the Jacobian matrix, evaluated at equilibrium of the virgin nutrient–prey–predator food chain, has to be zero or, when it oscillates, one extra Floquet multiplier evaluated for the stable limit cycle, has to be equal to one. The latter criterion is used in this paper to calculate the boundaries of the regions in the bifurcation diagram where the species compositions of the food web changes. The bifurcation software packages LOCBIF (Khibnik et al., 1993) and auto (Doedel and Kernévez, 1986; Doedel et al., 1997) were used. We consider Hopf bifurcation curves where the equilibrium becomes unstable and limit cycles originate when changing the bifurcation parameters, the dilution rate of the chemostat and the nutrient concentration in the inflowing medium.

Bifurcation analysis with the vital rates of the species (describing also their interaction) as free parameters yields regions of coexistence for various compositions of the food web. Such results can be used in community assembly theory. We use the species parameter set for bacterium-ciliate models, taken from Cunningham and Nisbet (1983) and Nisbet et al. (1983). We show that this allows some conclusions with respect to community assembly from the results for the simple small-scale food web. It appears that a predator can enforce two prey species to coexist in a large region of the bifurcation diagram, with the two control parameters of the chemostat as free parameters. A stable interior limit cycle can exist while there is no interior equilibrium. Furthermore, an invading competitor can stabilize an oscillating bi-trophic nutrient–prey–predator food chain.

Difficulties are reported in the literature (Hastings, 1996; Law and Morton, 1996; Morton and Law, 1997); (for instance, even though the equilibrium point is unstable, species can coexist on limit cycles or on more complicated trajectories) with the simplest application of the community assembly technique (Lotka–Volterra models with an unique stable interior equilibria worked out in Post and Pimm (1983) and Drake (1990)). Bifurcation analysis can be used to overcome these difficulties, even for more complex models, i.e.

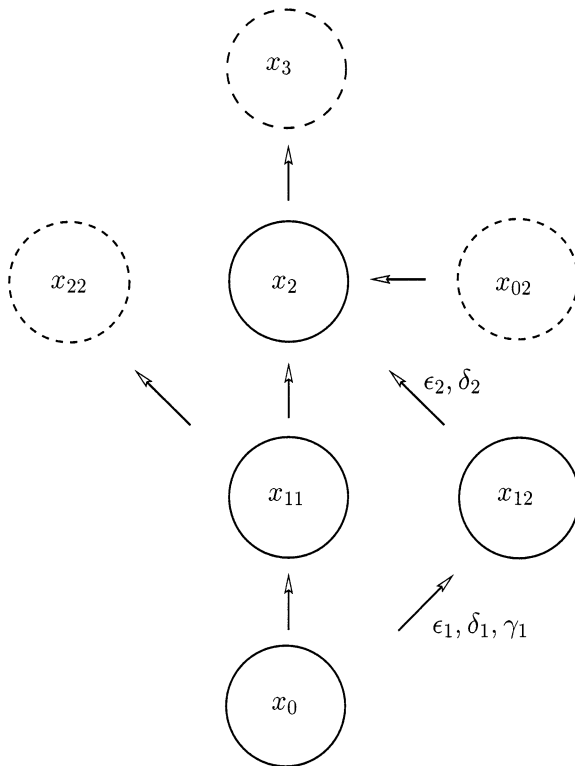


Fig. 1. Food web structure with different trophic levels, x_i , $i = 1, 2, 3$ and a non-growing nutrient, x_0 , at the base. The food web x_0, x_{11}, x_{12} and x_2 is studied in this paper. The influence of the top-predator x_3 is studied by Kooi et al. (1999), of a competitor predator x_{22} by Smith and Waltman (1994) and allochthonous input x_{02} by Huxel and McCann (1998).

Table 1

Parameters and state variables; t = time, m = biomass, v = volume of the reactor^a

Parameter	Dimension	Units	Interpretation
D	t^{-1}	h^{-1}	Dilution rate
$I_{(i-1)j,il}$	t^{-1}	h^{-1}	Maximum food uptake rate
$k_{(i-1)j,il}$	$m v^{-1}$	$mg dm^{-3}$	Saturation constant
M_{ij}	t^{-1}	h^{-1}	Maintenance rate coefficient
t	t	h	Time
x_0	$m v^{-1}$	$mg dm^{-3}$	Substrate density
x_{ij}	$m v^{-1}$	$mg dm^{-3}$	Biomass density
x_r	$m v^{-1}$	$mg dm^{-3}$	Substrate concentration in reservoir
$\mu_{(i-1)j,il}$	t^{-1}	h^{-1}	Maximum population growth rate

^a The first index denotes the trophic level, $i = 0$ substrate, $i = 1, j = 1, 2, l = 1, 2$, bacteria and $i = 2$ ciliate. Some parameters, for instance the saturation constants $k_{(i-1)j,il}$, have double indexes separated by a comma to emphasize that these quantities depend on two levels.

hyperbolic instead of linear functional responses. We discuss the applicability of the bifurcation analysis approach, focusing on invasion, in large-scale food webs as they can occur in the community assembly.

2. Description of the models

This section presents the food web model. The notation is introduced in Table 1. Let $x_0(t)$ denote the density of the resource (nutrient, substrate). Further, let $x_{ij}(t)$, $i = 1, 2, j = 1, \dots$ denote biomass densities of prey, $i = 1$ and predator, $i = 2$, respectively. Thus the first index, i , indicates the trophic level, $i = 0$ denoting the non-viable resource level. The second index, j , is a numbering of the different populations at the same (i -th) trophic level. When a trophic level consists of one species this second index is skipped. When two trophic levels are involved in the definition of a parameter, two indices will be used separated by a comma. For instance, in general $\mu_{uv,ij}$ denotes the

maximum growth rate of a predator x_{uv} , $u, v = 1, \dots$, feeding on the prey x_{ij} , $i, j = 1, \dots$. Before we introduce the model we will study, we first discuss some existing related models briefly to explain why we use a different formulation.

The interaction of two competing phytoplankton species x_{11} and x_{12} with Lotka–Volterra competition, and a zooplankton grazer x_2 introduced and studied by Kretzschmar et al. (1993) reads:

$$\frac{dx_{11}}{dt} = x_{11} \left(r_{11} \left(1 - \frac{x_{11}(t)}{K_{11}} - \frac{\beta_{11} x_{12}(t)}{K_{11}} \right) - \frac{I_{11,2}}{k_{11,2}} \frac{x_2}{1 + x_{11}/k_{11,2} + x_{12}/k_{12,2}} \right) \quad (1a)$$

$$\frac{dx_{12}}{dt} = x_{12} \left(r_{12} \left(1 - \frac{\beta_{12} x_{11}(t)}{K_{12}} - \frac{x_{12}(t)}{K_{12}} \right) - \frac{I_{12,2}}{k_{12,2}} \frac{x_2}{1 + x_{11}/k_{11,2} + x_{12}/k_{12,2}} \right) \quad (1b)$$

$$\frac{dx_2}{dt} = x_2 \left(\frac{\mu_{11,2}/k_{11,2} x_{11} + \mu_{12,2}/k_{12,2} x_{12}}{1 + x_{11}/k_{11,2} + x_{12}/k_{12,2}} - D_2 \right) \quad (1c)$$

where D_2 is the death rate of the predator and r_{1i} (intrinsic growth), K_{1i} (carrying capacity) and β_{1i} (competition coefficient) the Lotka–Volterra competition model parameters. The predator, x_2 , feeds on multiple prey species x_{1j} , $j = 1, 2$. The (scaled) functional response of a predator, x_{ij} on prey x_{uv} , is a partial Holling type II functional response function, denoted by $f_{uv,ij}$, with saturation constants $k_{uv,ij}$ and is given by

$$f_{uv,ij} = \frac{x_{uv}/k_{uv,ij}}{1 + \sum_w x_{uw}/k_{uw,ij}} \quad (2)$$

Omnivory is excluded and therefore we have $u = i - 1$.

Different mechanistic models are proposed by Metz and Diekmann (1986) for multiple nutrient uptake. In these models there are two parameters, the handling time and the search time. The quotient of the maximum ingestion rate and the saturation constant, I/k , is called the attack rate (Kretzschmar et al., 1993), or the search rate (Metz and Diekmann, 1986), and sometimes the searching efficiency (that is, number of prey encountered per unit of searching time (Arditi and Michalski, 1996)). The inverse of the saturation

constant, $1/k$, is the product of the search rate and the handling time. Then the functional response used in system (1) is obtained (see Metz and Diekmann, 1986). To simplify the analysis, the handling times are chosen to be equal for the predator consuming each prey, then $I_{12,2} = I_{11,2}$. Only the attack rates and the efficiencies or yields for the predator consuming the two prey species may differ.

The logistic equation describing the growth of a population on an inert nutrient can be derived from mass balance considerations (Kooi et al., 1998b). We found that the use of the logistic equation in combination with predation violates the conservation of mass. The same holds for the Lotka–Volterra competition model in combination with predation for it has the property that it collapses into the logistic if the prey species are identical. Therefore, we here reformulate the problem and model the resources explicitly.

With the Holling type II (hyperbolic) functional response also for the consumption of the nutrient by both prey species, instead of the Lotka–Volterra (linear) functional response, the governing equations for the nutrient–prey–competitor–predator system in the chemostat environment becomes

$$\frac{dx_0}{dt} = (x_r - x_0)D - I_{0,11}f_{0,11}x_{11} - I_{0,12}f_{0,12}x_{12} \quad (3a)$$

$$\frac{dx_{11}}{dt} = x_{11}(\mu_{0,11}f_{0,11} - D_{11}) - I_{11,2}f_{11,2}x_2 \quad (3b)$$

$$\frac{dx_{12}}{dt} = x_{12}(\mu_{0,12}f_{0,12} - D_{12}) - I_{12,2}f_{12,2}x_2 \quad (3c)$$

$$\frac{dx_2}{dt} = x_2(\mu_{11,2}f_{11,2} + \mu_{12,2}f_{12,2} - D_2) \quad (3d)$$

The depletion rate is the superposition of the dilution rate and the maintenance rate $D_{ij} = D + m_{ij}$. In Smith and Waltman (1994) these terms D_{ij} are called removal rates which may differ for different species. This occurs, e.g. when mortality is taken into account. When there is no maintenance, $m_{ij} = 0$, for all ij this Marr–Pirt model equates the Monod model.

Finally we introduce dissipated mass densities p_i expressed in the same units as the x_i

$$\frac{dp_{1j}}{dt} = x_{1j}((I_{0,1j} - \mu_{0,1j})f_{0,1j} + m_{1j}) - Dp_{1j} \quad (4a)$$

with $j = 1, 2$ and for the predator $i = 2$

$$\frac{dp_2}{dt} = x_2 \left(\sum_j (I_{1j,2} - \mu_{1j,2})f_{1j,2} + m_2 \right) - Dp_2 \quad (4b)$$

where we assume that these dissipated masses leave the reactor via the efflux with dilution rate D . The weighted total biomass density in the reactor may be defined by

$$H(t) = x_0(t) - x_r + \sum_{i=1}^2 \sum_j x_{ij}(t) + \sum_{i=1}^2 \sum_j p_{ij}(t) \quad (5)$$

where x_r is the substrate concentration in the reservoir. For this quantity $H(t)$ we have

$$\frac{dH}{dt} = -DH \quad (6)$$

As a consequence, $x_{ij}(t) \geq 0$, $i = 0, 1, 2$ and $p_{ij}(t) \geq 0$, $i = 1, 2$ are bounded for $t \geq 0$, and the system described by Eqs. (3a), (3b), (3c), (3d), (4a) and (4b) converges asymptotically to the invariant hyperplane $H = 0$.

When the parameters of both prey species are the same, that is the species are identical, the system reduces to a food chain with $x_1 = x_{11} + x_{12}$. Thus the model presented above fulfills the first consistency criterion formulated by Arditi and Michalski (1996). When one of the prey species x_{12} does not consume the resources ($I_{0,12} = 0 \Rightarrow \mu_{0,12} = 0$) and is not consumed by the predator ($I_{12,2} = 0 \Rightarrow \mu_{12,2} = 0$), the system reduces to a food chain with $x_1 = x_{11}$ while x_{12} is washed out. Also when the predator consumes both competing prey species, x_{12} goes to extinction when it does not consume the resources. These are degenerated cases for the second consistency criterion formulated by Arditi and Michalski (1996), namely that if the community splits into disconnected subwebs, then the system of equations separates into independent mathematical subsystems.

The parameters of the competitor, x_{12} , are perturbations of those for the prey, x_{11} . Perturbation parameters are introduced for the prey–nutrient interaction: ε_1 for the maximum growth rate, δ_1 for the saturation constant and γ_1 for the maximum ingestion rate, and for the predator–prey interaction: ε_2 and δ_2 , respectively. The ranges $\varepsilon_1 \in [-0.4, 0.4]$, $\delta_1 \in [-4, 8]$, $\varepsilon_2 \in [-0.1, 0.1]$, and $\delta_2 \in [-3, 3]$ represent biologically plausible values based on the experimental values given by Cunningham and Nisbet (1983), (Table 1) for micro-

bial bi-trophic food chains. For the sake of simplicity we take $I_{0,12} = I_{0,11}$ or $\gamma_1 = 0$, that is both prey consumes the common nutrient with the same rate.

3. Bifurcation analysis

Bifurcation analysis gives information about the long-term dynamic behavior of non-linear dynamic systems. The structural stability is studied with respect to so-called free or bifurcation parameters (Guckenheimer and Holmes, 1985; Kuznetsov, 1995). For a fixed composition of the species in the food web, the bifurcation parameters are the environmental parameters. In the chemostat case these are the dilution rate, D , and the concentration of nutrients in the influx, x_r , which are under control of the experimenter. The transcritical bifurcations are important for invasibility and Hopf bifurcations which mark the origin of limit cycles of the invaded system. In Table 2 the important bifurcation curves and points are listed.

The bifurcation curves were calculated with LOCBIF (Khibnik et al., 1993; Kuznetsov, 1995) and AUTO (Doedel and Kernévez, 1986; Doedel et al., 1997). These computer programs are implementations of a continuation technique which facilitate the study of the change of the position of the bifurcation points due to a change of free parameters. Starting at a point on a bifurcation curve, this curve is continued while test functions which are indicative of higher codimension bifurcation points are checked.

3.1. Calculation of the bifurcation diagrams

We explore the dynamics of system (Eqs. (3a), (3b), (3c) and (3d)) in the positive cone ($x_0 \geq 0, x_{11} \geq 0, x_{12} \geq 0, x_2 \geq 0$) $\in \mathbb{R}_+^4$. We will distinguish between a number of attractors given in Table 3. The first four rows indicate exterior attractors on the boundary of the positive cone. The latter row indicates the stable equilibrium and the stable limit cycle in the interior of the positive cone where all species coexist.

Table 2

List of all bifurcations, codimension-one curves and codimension-two points

Bifurcation	Description
<i>Codim-1 curves</i>	
$TC_{e,1j}$	Transcritical bifurcation: invasion through boundary equilibrium by prey ($j=1$) or competitor ($j=2$) in nutrient system
$TC_{e,2j}$	Transcritical bifurcation: invasion through boundary equilibrium by predator 2 in nutrient–prey ($j=1$) or nutrient–competitor system ($j=2$)
$TC_{e,3j}$	Transcritical bifurcation: invasion through boundary equilibrium $j=1$: prey invasion in nutrient–competitor–predator system $j=2$: competitor invasion in or nutrient–prey–predator system
$TC_{c,3j}$	Transcritical bifurcation: invasion through boundary limit cycle $j=1$: prey invasion in nutrient–competitor–predator system or $j=2$: competitor invasion in nutrient–prey–predator system
H_{2j}^-	Supercritical Hopf bifurcation for $j=1$: nutrient–prey–predator system $j=2$: nutrient–competitor–predator system food web becomes unstable and origin of stable limit cycle
H_3^-	Supercritical Hopf bifurcation for nutrient–prey–competitor–predator system: food web becomes unstable and origin of stable limit cycle
$Z_{e,2}$	Bifurcation with zero eigenvalues: extinction of the predator
<i>Codim-2 points</i>	
M_j	Codimension-two bifurcation points, $j=1, 2$
N	Codimension-two bifurcation point; invasion criterion holds for both prey and competitor

Table 3

Equilibria and limit cycles of the nutrient–prey–competitor–predator food web (Fig. 1)^a

	Equilibrium	Limit cycle
Nutrient	$E_0 = (\bar{x}_0, 0, 0, 0)$	
Nutrient–prey	$E_{11} = (\bar{x}_0, \bar{x}_{11}, 0, 0)$	
Nutrient–competitor	$E_{12} = (\bar{x}_0, 0, \bar{x}_{12}, 0)$	
Nutrient–prey–predator	$E_{11,2} = (\bar{x}_0, \bar{x}_{11}, 0, \bar{x}_2)$	$L_{11,2} = (\tilde{x}_0, \tilde{x}_{11}, 0, \tilde{x}_2)$
Nutrient–competitor–predator	$E_{12,2} = (\bar{x}_0, 0, \bar{x}_{12}, \bar{x}_2)$	$L_{12,2} = (\tilde{x}_0, 0, \tilde{x}_{12}, \tilde{x}_2)$
Nutrient–prey–competitor–predator	$E_{11,12,2} = (\bar{x}_0, \bar{x}_{11}, \bar{x}_{12}, \bar{x}_2)$	$L_{11,12,2} = (\tilde{x}_0, \tilde{x}_{11}, \tilde{x}_{12}, \tilde{x}_2)$

^a The bar denotes the equilibrium value of the state variable and the tilde their periodic fluctuations in the limit cycle case.

A bifurcation diagram is built up interactively where the user reacts on the intermediate results produced by the bifurcation package. With finding an equilibrium, integration in time of the ODE system with arbitrary but feasible initial conditions, gives a good starting point for a Newtonian method to solve the equilibrium equations. This (stable) equilibrium point is used as a starting point for continuation with one parameter as a free parameter. The continuation is performed until one of the test functions (for instance one that indicates a Hopf bifurcation) is zero. Thereafter, by taking an extra free parameter the (for instance Hopf) bifurcation curve can be calculated by continuation from that point, and so on.

A number of parameters (e.g. continuation step sizes) come with the implemented numerical algorithms while the numerical performance depends on these parameter values which sometimes have to be adjusted. Knowledge of bifurcation theory is necessary to interpret detailed intermediate results, to judge the correctness of the numerical results and to take the right decisions with continuation.

3.2. Description of the bifurcation diagrams

In what follows we will consider a specific competitor prey, x_{12} . The perturbation parameter values for this competitor are taken equal to $\varepsilon_1 = -0.08$, $\varepsilon_2 = 0.1$ and $\delta_1 = -2.5$, $\delta_2 = 0.1$. The perturbations are more or less arbitrary but the resulting maximum growth rates and the saturation rates are biologically plausible. The maximum growth rate of the competitor, $\mu_{0,12}$, is smaller ($\varepsilon_1 \leq 0$) than that of the prey, $\mu_{0,11}$, while

the maximum growth rate of the predator consuming the competitor, $\mu_{12,2}$, is larger ($\varepsilon_2 \geq 0$) than the maximum growth rate of the predator consuming the prey, $\mu_{11,2}$.

3.2.1. Nutrient–prey–competitor

We start with a discussion of the competition of the prey species consuming a common nutrient. This system, thus in the absence of the predator, $x_2 = 0$, is already dealt with extensively by Smith and Waltman (1994). Here we will confine ourselves to explaining the bifurcation diagram.

The bifurcation diagram of the nutrient–prey and the nutrient–competitor system is shown in Fig. 2. There are two transcritical bifurcation curves $TC_{e,11}$ and $TC_{e,12}$. These curves mark invisibility into the chemostat of the prey and competitor respectively. Point N is the intersection point of the two transcritical bifurcation curves $TC_{e,11}$ and $TC_{e,12}$.

Let $\mathcal{M}_{1j} = \mathcal{M}_{1j}(x_0)$, $j = 1, 2$, denote the actual specific growth rate of prey x_{1j} consuming the nutrient x_0 defined as:

$$\mathcal{M}_{1j}(x_0) = \left(\mu_{0,1j} \frac{x_0}{k_{0,1j} + x_0} - m_{1j} \right) \quad (7)$$

The critical dilution rate, denoted by D^* , where the asterisk denotes the critical value, is determined by the condition that the growth rate for the two competitors is the same. It forms together with the nutrient concentration $\bar{x}_0^*$, where the bar denotes the equilibrium value, the solution of the following two equations:

$$\mathcal{M}_{11}^{*def} = \mu_{0,11} \frac{\bar{x}_0^*}{k_{0,11} + \bar{x}_0^*} - m_{11} = D^* \quad (8a)$$

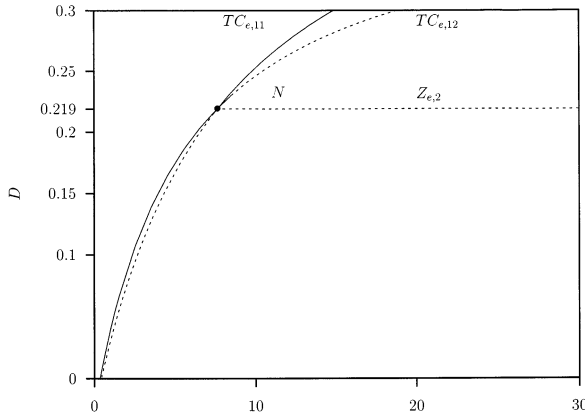


Fig. 2. Bifurcation diagram for Marr–Pirt model of nutrient–prey–competitor system ($x_2 = 0$): system (Eqs. (3a), (3b), (3c) and (3d)). The bifurcation parameters are the dilution rate D and the substrate concentration in reservoir x_r . Values assigned to physiological parameters and reference values for the perturbation parameters are listed in Table 4. The curves $TC_{e,11}$, $TC_{e,12}$ mark transcritical bifurcations. Point N is a codimension two point. The bifurcation curve $Z_{e,2}$ originates from this point. The solid parts of the transcritical bifurcation curves are relevant when both prey and competitor are possible invaders.

$$\mathcal{M}_{12}^{* \text{ def}} = \mu_{0,12} \frac{\bar{x}_0^*}{k_{0,12} + \bar{x}_0^*} - m_{12} = D^* \quad (8b)$$

At the codimension two point N we have $x_0 = \bar{x}_0^*$ and $\mathcal{M}_{11}^* = \mathcal{M}_{12}^* = D = D^* = 0.219$ where the parameter set given in Table 4 is used.

For $D = D^*$ there is coexistence. Then the right-hand sides of the Eqs. (3b) and (3c) with $x_2 = 0$, are zero because for both prey and com-

petitor the growth rate equates the dilution rates, see Eqs. (8a) and (8b). As a result, Eq. (3a) with right-hand side equal to zero is a linear relationship between the two unknowns $\bar{x}_{11}$ and $\bar{x}_{12}$, the equilibrium values for the prey and competitor, respectively. This shows that the solutions of the equilibrium equations form a one-dimensional manifold in the state space with constant $x_0 = \bar{x}_0^*$ given by Eq. (5) with $H = 0$:

$$x_r = \bar{x}_0^* + \frac{1}{D^*} \sum_j \frac{I_{0,1j} \bar{x}_0^*}{k_{0,1j} + \bar{x}_0^*} \bar{x}_{1j}^* \quad (9)$$

In the bifurcation diagram of the nutrient–prey–competitor system there is a bifurcation curve denoted by $Z_{e,2}$ where one eigenvalue equals zero. It originates from the codimension two point N , the intersection point of the two transcritical bifurcation curves $TC_{e,11}$ and $TC_{e,12}$.

When the dilution rate is above the critical value, $D > D^*$, the prey always wins and the relevant transcritical bifurcation curve is $TC_{e,11}$, while for $D < D^*$ the competitor always wins, that is, it establishes itself and eliminates the prey and the relevant transcritical bifurcation curve is $TC_{e,12}$.

3.2.2. Nutrient–prey–predator

In Fig. 3 we show the bifurcation diagram for the bi-trophic food chain, that is $x_{12} = 0$, calculated with the Marr–Pirt model (Eqs. (3a), (3b), (3c) and (3d)). The curves $TC_{e,11}$ and $TC_{e,21}$ are transcritical bifurcation curves and H_{21}^- marks a

Table 4

Parameter set for bacterium–ciliate models, after Cunningham and Nisbet (1983) and Nisbet et al. (1983)^a

Parameter	Unit	Values					
		$i = 1$		$i = 2$		$i = 3$	
		$l = 1$	$l = 2$	$j = 1$	$j = 2$		
$\mu_{(i-1)j,il}$	h^{-1}	0.5	$0.5 + \varepsilon_1$	0.2	$0.2 + \varepsilon_2$	0.15	
$k_{(i-1)j,il}$	mg dm^{-3}	8	$8 + \delta_1$	9	$9 + \delta_2$	10	
$I_{(i-1)j,il}$	h^{-1}	1.25	$1.25 + \gamma_1$	0.33	0.33	0.25	
m_i	h^{-1}	0.025	0.01	0.0075			

^a The values for the new parameters m_i are also given. The ranges for the control parameters are $0 < D < \mu_{0,11}$ and $0 < x_r \leq 300 \text{ mg dm}^{-3}$. The reference values for the perturbation parameters are: $\varepsilon_1 = -0.08$, $\varepsilon_2 = 0.1$ and $\delta_1 = -2.5$, $\delta_2 = 0.1$. Notice that $I_{0,11} \neq I_{0,12}$ is allowed but we take $\gamma_1 = 0$.

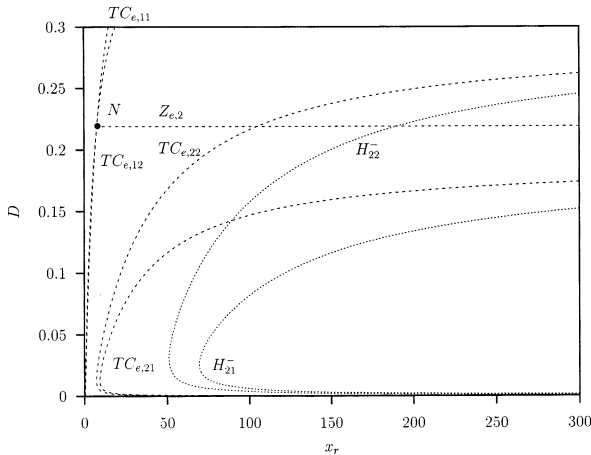


Fig. 3. Bifurcation diagram for Marr–Pirt model with two trophic levels: system (Eqs. (3a), (3b), (3c) and (3d)) for both the prey and competitor without competition. The bifurcation parameters are the dilution rate D and the substrate concentration in reservoir x_r . Values assigned to physiological parameters and reference values for the perturbation parameters are listed in Table 4. The curves $TC_{e,21}$, $TC_{e,22}$ are transcritical bifurcation curves and H_{21}^- , H_{22}^- mark supercritical Hopf bifurcation curves all for the bi-trophic food chains without and with perturbations of the vital rates.

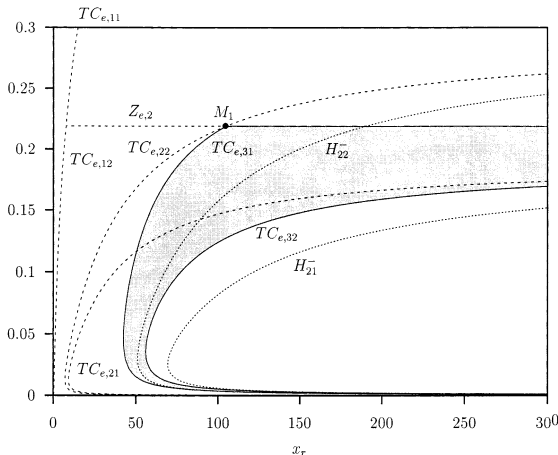


Fig. 4. Bifurcation diagram for Marr–Pirt model with two trophic levels: system (Eqs. (3a), (3b), (3c) and (3d)). The bifurcation parameters are the dilution rate D and the substrate concentration in reservoir x_r . Values assigned to physiological parameters and reference values for the perturbation parameters are listed in Table 4. The curves $TC_{e,31}$, $TC_{e,32}$ are transcritical bifurcation curves for the bi-trophic food web. Point M_1 is a codimension 2 point.

supercritical Hopf bifurcation curve. There are three biologically important regions; a region where the predator goes to extinction (left-hand side of $TC_{e,21}$), a region with a stable interior equilibrium (at the right-hand side of $TC_{e,11}$ and at the left-hand side of H_{21}^-) and a region where a stable interior limit cycle exists (to the right of H_{21}^-).

The attractors which occur in order by increasing the parameter x_r for any fixed values of D are:

$$E_0 \xrightarrow{TC_{e,11}} E_{11} \xrightarrow{TC_{e,21}} E_{11,2} \xrightarrow{H_{21}^-} L_{11,2} \quad (10)$$

The equilibria and periodic orbits are listed in Table 3.

3.2.3. Nutrient–competitor–predator

In the absence of the prey $x_{11} = 0$, the transcritical and the Hopf bifurcation curves are denoted by $TC_{e,12}$ and H_{12}^- respectively. These curves are also plotted in Fig. 3. The sequence of attractors that occur by increasing the parameter x_r for all D values is now:

$$E_0 \xrightarrow{TC_{e,12}} E_{12} \xrightarrow{TC_{e,22}} E_{12,2} \xrightarrow{H_{22}^-} L_{12,2} \quad (11)$$

With the parameter values used, the predator is able to invade the nutrient–competitor system for a smaller x_r value and the resulting nutrient–competitor–predator bi-trophic food chain starts to oscillate also for smaller x_r than in the nutrient–prey–predator case.

3.2.4. Nutrient–prey–competitor–predator

Now we discuss the bifurcation diagram for the whole food web including the predator, displayed in Fig. 4. In this picture two new transcritical bifurcation curves appear, namely $TC_{e,31}$ and $TC_{e,32}$, where the equilibrium values of prey and competitor biomass density respectively become zero. There is a codimension two point M_1 which is the intersection of the bifurcation curve $Z_{e,2}$ and the transcritical bifurcation curve $TC_{e,31}$. On the right-hand side of point M_1 the bifurcation acts as a transcritical bifurcation curve with respect to the predator for $D \uparrow D^*$, as well as a degenerated Hopf bifurcation curve where the imaginary part as well as the real part of the pair of complex conjugate eigenvalues converge to zero for $D \uparrow D^*$. Observe that the intersection

point of curve H_{22}^- with curve $Z_{e,2}$ is not a codimension 2 point, because $x_2 > 0$ for the Hopf bifurcation curve, H_{22}^- , while $x_2 = 0$ for the bifurcation curve, $Z_{e,2}$. Similar arguments hold true for the intersections of the curve $TC_{e,21}$ with the curves $TC_{e,31}$ and H_{22}^- . The three curves $Z_{e,2}$, $TC_{e,31}$ and $TC_{e,32}$, form the boundary of the region with an interior equilibrium.

The sequence, with increasing x_r , of attractors for $D > D^*$ is simply

$$E_0 \xrightarrow{TC_{e,11}} E_{11} \quad (12)$$

because sequence (Eq. (11)) cannot occur in the presence of x_{11} which out-competes x_{12} . For $D < D^*$ the sequence, with increasing x_r , of attractors is now:

$$E_0 \xrightarrow{TC_{e,12}} E_{12} \xrightarrow{TC_{e,22}} E_{12,2} \xrightarrow{TC_{e,31}} E_{11,12,2} \xrightarrow{TC_{e,32}} E_{11,2} \xrightarrow{H_{21}^-} L_{11,2} \quad (13)$$

Thus with predation, for small x_r values the competitor out-competes the prey but for larger x_r values the prey out-competes the competitor, while without predator the competitor always wins. This illustrates a top-down effect, namely that the presence of the predator influences the outcome of the competition between the two prey species.

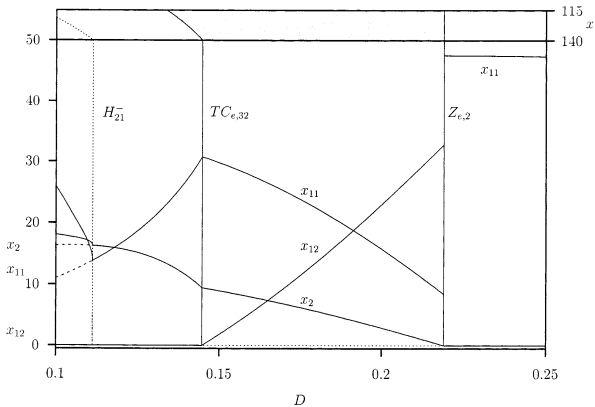


Fig. 5. One-parameter bifurcation diagram with peak values of the prey x_{11} , competitor x_{12} and predator x_2 . The bifurcation parameter is the dilution rate D . The concentration in the reservoir is $x_r = 140$. Solid curves give stable equilibrium values and peak values of stable limit cycles. Dashed curves give unstable equilibrium values. At the top the rotated two-parameter bifurcation diagram, Fig. 4 is plotted for $115 \leq x_r \leq 140$.

Fig. 5 gives the one-parameter bifurcation diagram where $x_r = 140$ is fixed and the consequences for the abundances of the species with changing the dilution rate, are displayed. The biomass densities for the two competing prey species x_{11} and x_{12} are discontinuous at $D = D^*$. Observe that for $D = D^*$ the equilibrium values for these two state variables are not unique and all points on the one-dimensional manifold given by Eq. (9) are equilibrium points. For $D > D^*$ the prey wins and we have $x_{12} = 0$ as well as $x_2 = 0$. Eq. (9) gives for $D > D^*$

$$\bar{x}_{11}^* = x_r - \bar{x}_0^* - D^* \frac{k_{0,11} + \bar{x}_0^*}{I_{0,11} \bar{x}_0^*} \quad (14)$$

The limit values for the biomass densities with $D \uparrow D^*$ will depend on the x_r values. When x_r possesses its value in point M_1 we have $\lim_{D \uparrow D^*} x_{11} = 0$ and there is a maximum discontinuity for both x_{11} and x_{12} with the transition over $D = D^*$. Eq. (9) gives now

$$\lim_{D \uparrow D^*} \bar{x}_{12}^* = x_r - \bar{x}_0^* - D^* \frac{k_{0,12} + \bar{x}_0^*}{I_{0,12} \bar{x}_0^*} \quad (15)$$

For a rather small value of D , $D \approx 0.0032$, the Hopf bifurcation curve H_{22}^- intersects the transcritical bifurcation curve $TC_{e,31}$ in another codimension two point, denoted by M_2 not shown in the Fig. 3. An expanded picture of this figure with the region around this point M_2 , is shown in Fig. 6. A supercritical Hopf bifurcation for the bi-trophic food web H_3^- originates from this point. Above this curve there is a stable interior equilibrium and below the curve the food web oscillates, i.e. there is a stable interior limit cycle. Also a transcritical bifurcation for limit cycles, denoted by $TC_{c,31}$, originates in point M_2 .

Fig. 7 shows the one-parameter bifurcation diagram with $x_r = 140$. With small values of D , the food chain in the absence of the prey starts to oscillate with the transition over the Hopf bifurcation curve H_{22}^- . With the transition over the transcritical curve $TC_{c,31}$ the prey invades and the resulting food web oscillates too. The x_{11} value of the associated unstable equilibrium is negative on the left-hand side of the curve $TC_{e,31}$ while the stable limit cycle is an interior attractor. The interior equilibrium on the right-hand side of the

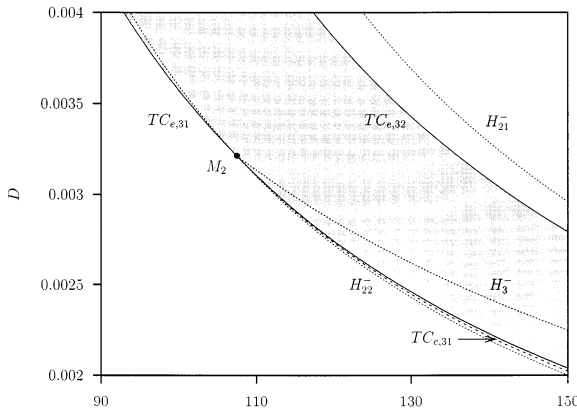


Fig. 6. Detail of the bifurcation diagram around the codimension two point M_2 . This figure is an expanded picture of Fig. 4. The curves $TC_{e,31}$, $TC_{e,32}$ are transcritical bifurcation curves and H_3^- marks a supercritical Hopf bifurcation curve for the bi-trophic food web.

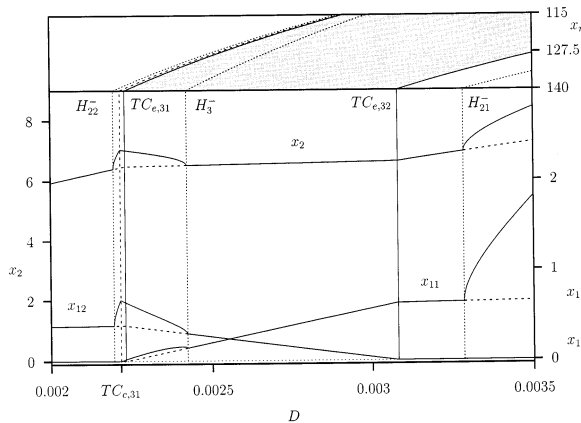


Fig. 7. One-parameter bifurcation diagram with peak values of the prey x_{11} , competitor x_{12} and predator x_2 . The bifurcation parameter is the dilution rate D . The concentration in the reservoir is $x_r = 140$. Solid curves give stable equilibrium values and peak values of stable limit cycles. Dashed curves give unstable equilibrium values. At the top the rotated two-parameter bifurcation diagram, Fig. 6 is plotted for $115 \leq x_r \leq 140$.

curve $TC_{e,31}$, becomes stable with the transition over the Hopf bifurcation curve H_3^- . The attractors that occur in order by increasing the parameter D , where the fixed x_r value is larger than at point M_2 , are now:

$$\begin{aligned} E_0 &\xrightarrow{TC_{e,12}} E_{12} \xrightarrow{TC_{e,22}} E_{12,2} \xrightarrow{H_{22}^-} L_{12,2} \xrightarrow{TC_{e,31}} L_{11,12,2} \xrightarrow{H_3^-} E_{11,12,2} \rightarrow \\ &TC_{e,32} E_{11,2} \rightarrow L_{11,2} \end{aligned} \quad (16)$$

This completes the description of the bifurcation diagram Fig. 4. We want to stress that for other parameter values the general picture of the bifurcation diagrams can be different from the one presented in this section, but the same type of attractors can occur. The rich set of possible web structures seen here is a consequence of choice of the parameter values such that the critical value for the dilution rate is in the range between the maximum growth rates of the predator consuming the prey and competitor: $\mu_{11,2} < D^* < \mu_{12,2}$.

4. Invasibility and community assembly

In the Appendix A it is shown that a species can invade a system if its per capita growth rate is larger than its depletion rate with its population size zero while the other species are at their equilibrium values. When the virgin system cycles along periodic orbit the mean value along the limit cycle of the per capita growth rate has to be larger than the mean value of the depletion rate. When a species from the pool is allowed to invade the community, time integration reveals to which attractor the system will evolve. This attractor is the starting point for the next invasion to occur.

The uninvadable endpoint of the food web assembly is unique when the prey, the competitor and the predator are all possible invaders. The sequence of food web compositions during the assembly process starting with the nutrient, depends of course on the sequence of species invasions employed.

The results obtained in the previous section can be summarized as follows. For dilution rates above the critical value, $D > D^*$, the predator is not able to invade, that is, the prey always out-competes the competitor. For $D < D^*$ in the region on the left-hand side of the curve $TC_{e,31}$ the competitor out-competes the prey whether the predator is absent or present (left- or right-hand side of the curve $TC_{e,22}$, respectively). However, in the region on the right-hand side of $TC_{e,32}$ the prey establishes itself and replaces the competitor in the presence of the predator while in the ab-

sence of the predator the competitor wins. Between the curves $TC_{e,32}$, $Z_{e,2}$ and H_{22}^- the prey invades and stabilizes the oscillating nutrient–competitor–predator system.

The results presented in the bifurcation diagrams are for the perturbation parameter values given in Table 4. As already stated, for other parameter values different bifurcation pictures will occur. An important quantity is the critical value D^* which depends on the physiological parameters of the prey species consuming the nutrient, the parameters ε_1 and δ_1 , but does not depend on the parameters ε_2 and δ_2 (see Eqs. (8a) and (8b)). In the bifurcation analysis the codimension 2 point N can be continued where D together with ε_1 and δ_1 are the free parameters. As already mentioned, we assume that $I_{0,11} = I_{0,12}$ or $\gamma_1 = 0$, for simplicity sake.

In Fig. 8 the feasible region in the $(\mu_{0,12}, k_{0,12})$ -plane for the critical values $0 \leq D^* \leq 0.3$ is shown. These curves are calculated as follows. First the $\bar{x}_0^*$ is calculated with Eq. (8a) and the result is substituted in Eq. (8b) where D^* has a specific value. This yields a linear relationship between $\mu_{0,12}$ and $k_{0,12}$. The maximum value for D^* is the maximum growth rate of the predator consuming prey or competitor. This is a conserva-

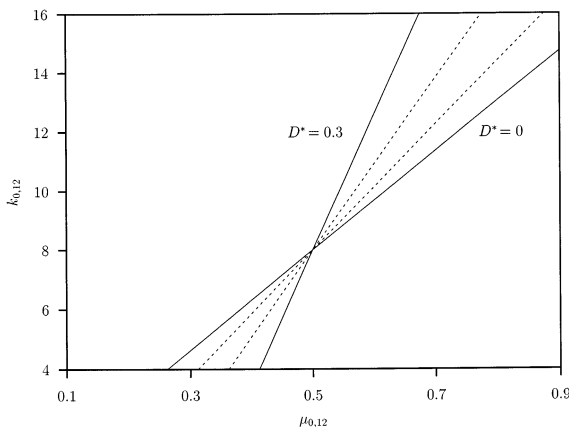


Fig. 8. The feasible region for the critical values in the $(\mu_{0,12}, k_{0,12})$ parameter plane. In the point (0.42, 5.5) the critical parameter value is $D^* = 0.219$. The solid lines give the boundaries of the regions where the predator can invade, $D^* = 0.0$ and $D^* = 0.3$. The dashed lines are for intermediate values: $D^* = 0.1$ and $D^* = 0.2$.

tive upperbound for the dilution rate where the food web can possess an interior attractor; a more refined estimation would be: $\max_i(\mu_{1,i,2} - m_2)$.

Fig. 8 shows that only in a relative small region of the parameter space an interior attractor can exist. Outside that region the two transcritical bifurcation curves shown in Fig. 3 do not intersect in the relevant region, and therefore one of the prey species will win for all dilution rates. To which attractor the system actually will evolve depends of course on the control parameter values, D and x_r , but also on the remaining free parameters $I_{0,12}$, $\mu_{12,2}$, $k_{12,2}$ where $\mu_{11,2}$, $k_{11,2}$ are fixed.

5. Discussion and conclusions

Smith and Waltman (1994) discuss the asymptotic behavior of a nutrient and two competing prey species. Competitive exclusion holds, that is, generally one prey out-competes the other. It is shown here that when the dilution rate has a critical value, a one-dimensional manifold forms a set of equilibria. It depends on the initial condition to which point on this manifold the system converges. We here showed that a predator can prevent competitive exclusion. In the presence of a predator the critical value marks a bifurcation point where the biomass densities of the species can be discontinuous when changing the dilution rate.

The endpoint of the food web assembly is unique when the prey, the competitor and the predator are all possible invaders. This agrees with the finding reported by Morton et al. (1996) where the linear instead of the hyperbolic functional response is used, namely that for pools with a small number of species, multiple endpoints are rare.

In a very small part of the diagram the nutrient–prey–competitor–predator shows cyclic behavior. We did not find chaotic attractors but we stress that the bifurcation diagrams presented here hold for the parameter setting given in Table 4. For other vital parameters of the species which build up the food web, a cascade of flip bifurcations may lead to a chaotic behavior. Klebanoff

and Hastings (1994) and Vandermeer and Maruca (1998) found that chaotic behavior was present for similar two prey–predator models. However, the model studied by Klebanoff and Hastings (1994), and also mentioned by Hastings (1996), violates the property of invariance formulated by Arditi and Michalski (1996).

A stable interior limit cycle with negative biomass densities in the unstable equilibrium, is impossible in the Lotka–Volterra model formulation and is therefore a consequence of the Holling type II functional response for the interaction of the species. This illustrates also that invasion in models with hyperbolic functional response has to be treated differently than invasion in models with linear functional response.

The small-scale food web discussed in this paper consists of heterotrophs with an allochthonous input at the basal trophic level. The population dynamics is described by an unstructured model (that is, all individuals are taken identical or their state is described by mean values, as is appropriated in microorganisms), there is no spatial structure (that is, the environment is homogeneous as is the case in the chemostat system). Despite these simplifications, it is tempting to extrapolate the results obtained for large-scale food webs in nature.

For large-scale food web models containing many state variables and many parameters it is impractical to calculate the full bifurcation diagram with respect to all types of nutrient import and export rates. The calculation of the different points of bifurcations may be troublesome due to the large dimension of the underlying, often stiff, non-linear dynamic system.

By way of example, it may be difficult to find all equilibria when there are multiple equilibria as they occur when the functional response is hyperbolic. Integration in time of the ode system may not yield a good starting point for a Newtonian method to solve the equilibrium equations when the basins of attraction are complex regions in the state space. It is possible to start with a food chain where at each trophic level all populations are lumped into one with parameter values equal the average parameter value. For a food chain there is a technique which reduces the whole system of equations to a single equation so that all the possible

equilibria can be found rather easily. Suppose that x_0 is known, then $x_1, x_2, \dots$ can be calculated explicitly and the equilibrium equation for the top-predator gives an equation with x_0 as the unknown. Checking the whole feasible region $0 < x_0 \leq x_r$ yields all the interesting equilibria. Subsequently, application of a continuation method gives the equilibria of the food web.

Available bifurcation analysis computer packages are able to detect only points of a very restricted codimension (up to 4). This illustrates that for large-scale food webs there are too many parameters to give a complete classification of the dynamic behavior. A complete description of all possible uninvadable endpoints of a community assembly is even more difficult. In addition, in practice the parameters associated with the numerical algorithms (tolerances, continuation step size and discretization constants) have to be adjusted interactively by the user, using intermediate results. In conclusion, it seems impossible to generate complete bifurcation diagrams in a stand-alone process.

This leads us to the question whether it is necessary to generate this detailed information for all possible intermediate as well as uninvadable endpoint food webs. For the ecological community assembly approach this is not necessary, and we propose, similar to that used with for the Lotka–Volterra system by Law and Morton (1996), to concentrate on invasion (immigration by populations with finite size excluding) and subsequent convergence to an interior attractor.

Invasibility can be checked (Appendix A) and if invasion is successful, numerical integration in time will thereafter yield the attractor to which the resulting food web will converge. This process can be repeated iteratively. When the attractor is close to a bifurcation point the asymptotic behavior may be very slow in which case bifurcation analysis can give additional information. Furthermore, there can be long lasting transient behavior, as pointed out by Hastings (1996). Transient chaotic behavior is associated in Boer et al. (1999) with the existence of global homoclinic bifurcations to a saddle limit cycle for a tri-trophic food chain that is similar to the one discussed by Hastings (1996). When chaos is detected, the bifur-

cation diagram has to be studied, especially the occurrence of global bifurcations in the region of interest. Boer et al. (1998) continue global bifurcations in the parameter space for the tri-trophic food chain in the chemostat (with the parameter values as given in Table 4).

In the case of fluctuating environments numerical integration is perhaps the only way to go. In the chemostat case the two control parameters D and x_r become functions of time and it is well known that complex dynamics can occur already with a simple nutrient–prey–predator system (Kot et al., 1992; Pavlou and Kevrekidis, 1992). For the food web studied in this paper, it would be interesting to study its dynamic behavior where the dilution rate fluctuates around the critical value. In the period where $D > D^*$ the competitor goes to extinction but in the period with $D < D^*$ it establishes itself again. This suggests that the abundances can oscillate with large amplitudes.

It is a challenge to apply this technique based on non-linear dynamics system theory, to large-scale food webs. Aggregation methods (Iwasa et al., 1987, 1989; Auger and Poggiale, 1998) can be applied to reduce the dimension of the system when there is a large difference in time-scales between the trophic levels. Body size scaling relationships proposed by Kooijman (2000), where all the physiological parameters of the species scale with the maximum body size of the species, can be used to keep the number of parameters as small as possible.

May (1973) states that randomly introduced complexity destabilizes complex systems. This counter-intuitive result mainly rests on the linear functional response properties of the equations that he used. More realistic non-linear functional response shows the opposite (see recent papers by Polis (1998) and McCann et al. (1998)). We here showed that the invasion of a competing prey, so an increase in complexity, can stabilize the very simple trophic system.

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Appendix A. Invasion of a competitor in a bi-trophic food chain

In this appendix we derive invasibility conditions for a competitor to invade a bi-trophic food chain. The procedure is similar to the one proposed by Smith and Waltman (1994) and was also used by Kooi et al. (1999) where we derived the invasion criterion for a top-predator in a bi-trophic food chain. The results obtained agree with those mentioned by Law and Morton (1996).

We start with invasion from a boundary equilibrium which is assumed to be stable. For example, on the left side of the Hopf bifurcation curve H_2^- in the Fig. 3. The stable equilibrium of the virgin bi-trophic food chain is denoted by

$$E_{11,2} = (\bar{x}_0 \quad \bar{x}_{11} \quad \bar{x}_2 \quad \bar{x}_{12} = 0)^T \quad (A1)$$

Let $\mathcal{J}$ denote the 3×3 Jacobian matrix for the virgin bi-trophic food chain and $\mathcal{J}$ be a 4×4 Jacobian matrix for the invaded bi-trophic food chain, both evaluated at $E_{11,2}$

$$\mathcal{J} = \begin{pmatrix} \mathcal{J} & -I_{0,12}\bar{f}_{0,12} & -I_{11,2}\bar{f}_{11,2}\bar{x}_2 \\ & (\mu_{11,2}\bar{f}_{11,2} + \mu_{12,2}\bar{f}_{12,2})\bar{x}_2 & \\ 0 & 0 & 0 & \bar{\mathcal{M}}_{11,2} - D \end{pmatrix} \quad (A2)$$

where

$$\bar{f}_{i-1,i} = f_{i-1,i}(\bar{x}_0, x_{11}, \bar{x}_2) \text{ and}$$

$$\bar{f}_{i-1,2} = \frac{df_{i-1,2}}{dx_{12}}(\bar{x}_{11}, \bar{x}_2)$$

and the specific growth rate of the invader $\bar{\mathcal{M}}_{11,2} = \mathcal{M}(\bar{x}_0, \bar{x}_{11}, \bar{x}_2)$ with $\mathcal{M}$ defined as

$$\mathcal{M}(x_0, x_{11}, x_2) = \left(\mu_{0,12} \frac{x_0}{k_{0,12} + x_0} - \frac{I_{12,2}k_{11,2}}{k_{12,2}} \frac{x_2}{k_{11,2} + x_{11}} - m_{12} \right) \quad (A3)$$

Observe that the specific growth rate of the invading species into the virgin environment depends on the abundances of its nutrient, predator, but also on its competitor. Growth is enhanced by

more food and less predators, but also by more prey. The latter fact seems to be surprising, more prey being also advantageous for the invader.

Substitution of the expressions for $\bar{x}_0$, $\bar{x}_{11}$ and $\bar{x}_2$ into $\bar{\mathcal{M}}_{11,2} = D$, through Eq. (A3), gives the transcritical bifurcation curve $TC_{e,32}$ being a relationship between D and x_r .

Expanding the determinant of matrix $\mathcal{J} - \lambda I$, where I is the 3×3 identity matrix we find

$$\det(\mathcal{J} - \lambda I) = \det(\mathcal{J} - \lambda I) \times (\bar{\mathcal{M}}_{11,2} - D - \lambda) \quad (\text{A4})$$

Hence, besides the three eigenvalues of the matrix $\mathcal{J}$ with negative real parts (by assumption of a stable equilibrium $E_{11,2}$ of the virgin bi-trophic food chain), there is one additional eigenvalue, namely $\bar{\mathcal{M}}_{11,2} - D$. The zero-crossing of the latter expression is the test-function for the transcritical bifurcation $TC_{e,32}$. In these points the growth rate of top predator $\bar{\mathcal{M}}_{11,2}$ equals just the depletion rate D . When the specific growth rate $\bar{\mathcal{M}}_{11,2}$ is greater than the depletion rate D the equilibrium $E_{11,2}$ becomes unstable. As a result the top predator can invade. Hence, the invasibility condition reads $\bar{\mathcal{M}}_{11,2} > D$.

For the derivation of the invasion via boundary limit cycles (for example on the right-hand side of the Hopf bifurcation curve H_2^- in the bifurcation diagram Fig. 3) the reader is referred to Kooi et al. (1999). The invasion criterion reads:

$$T_0^{-1} \int_0^{T_0} \bar{\mathcal{M}}_{11,2}(t) dt > D \quad (\text{A5})$$

where T_0 is the period of the stable periodic orbit of the virgin bi-trophic food chain and the per capita growth rate of the invader $\bar{\mathcal{M}}_{11,2}(t) = \mathcal{M}(\bar{x}_0(t), \bar{x}_{11}(t), \bar{x}_2(t))$ evaluated along the periodic orbit $\bar{x}_0$, $\bar{x}_{11}$, $\bar{x}_2$. The transcritical bifurcation $TC_{e,31}$ (Fig. 6) was calculated using this criterion.

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