Studies in Mathematical Sciences Vol. 2, No. 1, 2011, pp. 157-182 www.cscanada.org

## On the Stability-complexity Relation for Unsaturated Semelpareous Discrete Food-chains

## Torsten Lindström<sup>1,\*</sup> Gunnar Söderbacka<sup>2</sup>

**Abstract:** In this paper we formally prove that invading carnivores in the discrete food-chain derived and preliminary analyzed in [2] always makes the system less stable and thus, limit the food-chain length in the corresponding system. Hence, invading unsaturated carnivores are not able to stabilize oscillatory dynamics. What we prove constitutes a significant difference between discrete and continuous food-chains. Actually, Freedman and Waltman<sup>[3]</sup> related the stabilizing properties of an invading carnivore in continuous food-chains to absence of saturation: An unsaturated carnivore keeps at least one interior equilibrium - if one exists - locally stable. One consequence is that the dynamics of unsaturated discrete food-chains display similarities with saturated continuous food-chains. Indeed, discrete dynamics seem to have a similar destabilizing impact on the dynamics as saturation has.

Key Words: Stability-complexity relation; Discrete food-chains

## 1. INTRODUCTION

Central paradigms regarding food-web complexity versus stability were called into question using simple models by May<sup>[1]</sup>. The results therein indicated that stability and possibilities for species persistence do not in general increase with food-web complexity. The numerical results given in [2] indicated that the same conclusion holds in discrete food-chains related to seasonal environments giving rise to continuous deathand predation processes and discrete birth processes. In this paper we prove that this numerical observation holds analytically. Although some results asking for reassessment of May's classical results have appeared later, most results are numerical and lack the general validity expressed in classical works<sup>[4]</sup>.

What we prove in this article constitutes one major difference between discrete and continuous foodchains. Rosenzweig<sup>[5]</sup> noted that continuous food-chains may display both stabilizing and destabilizing scenarios. We prove that stabilizing scenarios<sup>[3, 18]</sup> related to unsaturated invading carnivores are excluded in discrete systems. This is one of the most important expectations implied by the results in [2]. The ecological consequence of these results is that food-chains are expected to be shorter in seasonal and boreal environments giving rise to pulse wise births. This difference may be a part of the explanation of the differences between food-chain lengths in marine and terrestrial environments, and rain forests versus arctic

<sup>&</sup>lt;sup>1</sup>School of Computer Science, Physics and Mathematics, Linnaeus University, SE-39182 Kalmar, Sweden. E-mail address: torsten.lindstrom@lnu.se.

<sup>&</sup>lt;sup>2</sup>Avdeling for Nærings-og sosialfag, Høgskolen i Finnmark, Follumsvej, N-9509 Alta, Norway.

E-mail address: Gunnar.Soderbacka@hifm.no.

<sup>\*</sup>Corresponding author.

<sup>&</sup>lt;sup>†</sup>Received 10 December 2010; accepted 4 February 2011.

and boreal fauna<sup>[6]</sup>.

We think it is important to give a formal proof for how the stability complexity relation works in discrete ecosystems, since only such proofs have the potential to close future discussions of whether there still might be parameter values predicting other or exceptional scenarios not included in the discussion here. No parameter values of any ecological relevance are left outside the discussion here. But, of course, no mathematical proof whatsoever can close the discussion on whether other modeling assumptions might alter the predictions. In any case, we think the discussion in the future is simplified; after this one can concentrate the efforts on what mechanisms might alter the model predictions.

The proof of the above mentioned result is technical and based on a variety of quite precise estimates. The structure of the proof can probably be improved in the future, but we think it is essential to document the proof of this fact at this stage so that future generations can concentrate on improving the method of proof or making its implications visible for larger audiences and not on finding out how the basic relations work in this system.

The precision required in the estimates in order to obtain the requested results is high and is illustrated by the fact that one of the estimates turned out to be the Padé-approximation<sup>[7]</sup> of a certain transcendental function. Here we make use of the fact that Padé-approximations are usually known for producing precise estimates on surprisingly large intervals. The methods used are mainly those of dynamical systems<sup>[8]</sup> and bifurcation theory<sup>[9]</sup>. The major idea is a change of parameters in the relevant parts of the parameter space. We formulate our main results in Section 3 as two theorems, one theorem stating the stability-complexity relation for the system in question (Theorem 4.1) and one stating the structure of the bifurcation diagram of the system under consideration (Theorem 4.3).

## 2. THE MODEL

We work throughout the paper with the discrete food-chain model

$$X_{t+1} = \frac{M_0 X_t e^{-U_t}}{1 + X_t \max(e^{-U_t}, \kappa(U_t)\kappa(Z_t))},$$
  

$$U_{t+1} = M_1 X_t U_t e^{-Z_t} \kappa(U_t) \kappa(M_2 U_t Z_t),$$
  

$$Z_{t+1} = M_2 U_t Z_t,$$
(1)

where  $M_0, M_1, M_2 > 0$ , and

$$\kappa(\gamma) = \begin{cases} \frac{1 - e^{-\gamma}}{\gamma}, & \gamma > 0, \\ 1, & \gamma = 0. \end{cases}$$
(2)

The system is considered for non-negative values of the variables  $X_t$ ,  $U_t$ ,  $Z_t \ge 0$ . The variable  $X_t$  denotes the vegetation level,  $U_t$  is related to the herbivore level through a nonlinear transformation, and  $Z_t$  denotes the carnivore level. The parameter  $M_0$  is related to the growth rate of the vegetation level, the parameter  $M_1$ is related to the growth and search rates of the herbivores, and the strength of competition at the vegetation level, whereas the last parameter growth and search rates of the carnivores and the search rates at the herbivore level. For details of derivation of model and parameter implementation, see [2]. The main assumptions are that the two higher trophic levels are both unsaturated and that all trophic levels are semelpareous, all individuals reproduce only once upon their life-time. The first assumption is clearly unrealistic, on the other hand the unsaturated case must be well understood before saturated cases can be considered. Such cases must probably be studied using techniques from impulsive system theory<sup>[10–12]</sup>. The last assumption is particularly suitable for terrestrial arthropods, see [13].

## 3. GENERAL BEHAVIOR OF FIXED POINTS AND BASIC DYNAMICAL BEHAVIOR

The system has at most four fixed points  $P_0 = (0, 0, 0)$ ,  $P_1 = (M_0 - 1, 0, 0)$ ,  $P_2$  in the coordinate plane Z = 0and  $P_3$  not in any coordinate plane. That is, one fixed point corresponding to each possible length of the food-chain. We consider bifurcations of fixed points in the  $M_0M_1$ -space  $(M_0, M_1 > 0)$  for fixed  $M_2$  and introduce the following notation:

**Definition 3.1** (Notation D, E, and  $F_2$ ) We denote the curve

$$M_1 = f_2(M_0) = 1/(M_0 - 1), M_0 > 1,$$

by  $F_2$ . The region  $0 < M_0 < 1$  is denoted by E and the region where  $M_0 > 1$  and  $M_1 < f_2(M_0)$  is denoted by D.

#### **3.1** Type of Fixed Points $P_0$ and $P_1$

We next link the newly defined regions to the local stability of the fixed points mentioned above. The fixed point  $P_0$  exists for any values of the parameters and the Jacobian matrix at the point is diagonal with elements  $M_0$ , 0, 0. Thus,  $P_0$  is

- stable for  $M_0 < 1$  (that is in *E*) and
- saddle with dim  $W^s(P_0) = 2$  for  $M_0 > 1$ .

The fixed point  $P_1$  exists for  $M_0 > 1$  and the Jacobian matrix at the point is triangular with elements  $1/M_0$ ,  $M_1(M_0 - 1)$ , 0 at its main diagonal. Thus,  $P_1$  is

- stable for  $1 < M_0 < 1 + 1/M_1$  (that is in D) and
- saddle with dim  $W^s(P_1) = 2$  for  $M_0 > 1 + 1/M_1$  (which is equivalent to  $M_1 > f_2(M_0)$ ).

We summarize the local behavior around the fixed points  $P_0$  and  $P_1$  as follows: (a) In region E only  $P_0$  exists and there it is stable. (b) In region D both  $P_0$  and  $P_1$  exist and  $P_0$  is saddle with dim  $W^s(P_0) = 2$  and  $P_1$  is stable. (c) In the remaining areas (to be defined below) of the parameter space  $(M_0 > 1, M_1 > f_2(M_0))$  both  $P_0$  and  $P_1$  are saddles and dim  $W^s(P_i) = 2$ , i = 0, 1.

#### **3.2** Type of Fixed Point *P*<sub>2</sub>

We continue splitting the parameter space into regions determined by the local behavior of the fixed points. The next areas will be related to the local behavior of  $P_2$ .

**Definition 3.2** (Notation C and  $F_3$ ) We denote the curve

$$M_1 = f_3(M_0) = 1/(M_0 e^{-u_3} - 1), M_0 > e^{u_3}, u_3 = 1/M_2,$$

by  $F_3$ . The region between  $F_2$  and  $F_3$  we denote by C.

Note that  $f_3(M_0) > f_2(M_0)$  for  $M_0 > e^{u_3}$ . Negative branches of this curve was left outside consideration in our definition, so this relation holds for all  $u_3 > 0$ . The fixed point  $P_2$  exists for  $M_0 > 1 + 1/M_1$  (that is

above  $F_2$ , so the exchange of stability of  $P_1$  coincides with the birth of the fixed point  $P_2$ ) and in coordinates it is given by

$$(x_2, u_2, 0) = \left(\frac{w \ln w}{M_1(w - 1)}, \ln w, 0\right),$$
$$w = \frac{M_0 M_1}{M_1 + 1}.$$
(3)

where

The Jacobian matrix at  $P_2$  takes the form

$$J(P_2) = \begin{pmatrix} \frac{M_1}{M_1 + 1} & -\frac{x_2}{u_2} \frac{M_1 u_2 + M_1 x_2 - 1}{M_1 + 1} & \frac{x_2}{2(M_1 + 1)} \\ u_2/x_2 & M_1 x_2 - u_2 & -u_2 \left(1 + \frac{M_2 u_2}{2}\right) \\ 0 & 0 & M_2 u_2 \end{pmatrix},$$

(cf. [2]). Let J' be the submatrix got from  $J(P_2)$  excluding the last row and column. Then

$$\det(J') = h - \frac{1}{M_1 + 1},$$

where

$$h = \frac{w \ln w}{w - 1}.\tag{4}$$

and w was defined above by (3). The function h turns out to be a central auxiliary function later on. We need the following properties of h:

Lemma 3.3 Consider the function h defined by (4). It has the following properties:

- (a) *h* is increasing in w for w > 1;
- (b) the derivative h' is decreasing in w for w > 1;
- (c)  $\lim_{w\to 1_+} h = 1$  and  $\lim_{w\to\infty} h = \infty$ ;
- (d) there is a unique number  $w_{max}$  such that  $h(w_{max}) = 2 (w_{max} \approx 4.922)$  for w > 1;
- (e) *h* is defined on  $[e^{u_3}, w_{max}]$  if  $0 < u_3 < u_{max} = \ln w_{max}$  and  $h([e^{u_3}, w_{max}]) = [1/\kappa(u_3), 2] \subset [1, 2]$ .

The proof of Lemma 3.3 can be found in Section 7. For det(J') = 1 we get a Neimark-Sacker bifurcation and we introduce:

**Definition 3.4 (Notation NS2)** *The Neimark-Sacker bifurcation curve for*  $P_2$  *in the*  $M_0M_1$ *-space is called the* NS2*-curve.* 

Note that det(J') = 1 (NS2-curve) is equivalent to

$$h = \frac{M_1 + 2}{M_1 + 1},\tag{5}$$

from which we get

$$M_1 = \frac{2-h}{h-1}$$
, and  $M_0 = \frac{w}{2-h}$ . (6)

It follows from Lemma 3.3 that  $1 < w < w_{max} \sim 4.922$  will be the range of definition of the NS2-curve in w. Further, we note that  $M_0$  is increasing in w and that  $M_1$  is decreasing in w. It follows that  $M_0 \rightarrow \infty$ and  $M_1 \rightarrow 0$  for  $w \rightarrow w_{max}$  and  $M_0 \rightarrow 1$  and  $M_1 \rightarrow \infty$  for  $w \rightarrow 1$  (Lemma 3.3(c)-(d)). Thus, we take w as an parameter for describing the NS2-curve (5) in the  $M_0M_1$ -parameter space. Note that w = 1 on  $F_2$  and  $w = e^{u_3} > 1$  on  $F_3$ . Intersections between the defined curves therefore become readable and we introduce a useful number: Let

$$u_{max} = \ln w_{max}.\tag{7}$$

Alternatively, we may define  $u_{max}$  using (5) directly as the solution to

$$2 = \frac{u_{max}e^{u_{max}}}{e^{u_{max}} - 1} = \frac{1}{\kappa(u_{max})}.$$
(8)

Now put  $\tilde{M}_2 = 1/u_{max} \sim 0.63$ . The NS2-curve intersects  $F_3$  if  $M_2 > \tilde{M}_2$  otherwise it is wholly in C. It divides region C into two parts. We introduce:

**Definition 3.5 (Notation** C(1) **and** C(3)) *We denote by* C(3) *the part of* C (cf. Definition 3.2) *having*  $F_2$  *in its boundary and the other part by* C(1).



**Figure 1:** Bifurcation diagram in the  $M_0M_1 - plane$  when  $M_2 = 0.5$ . These are the typical features of a bifurcation diagram of (1) as long as  $M_2 < \tilde{M}_2 \sim 0.63$ 



**Figure 3:** Bifurcation diagram in the  $M_0M_1 - plane$  when  $M_2 = 2$ 



**Figure 2:** Bifurcation diagram in the  $M_0M_1 - plane$  when  $M_2 = 1$ . These are the typical features of a bifurcation diagram of (1) as long as  $0.63 \sim \tilde{M}_2 < M_2 < M_2^* \sim 1.344$ 



**Figure 4:** Bifurcation diagram in the  $M_0M_1 - plane$  when  $M_2 = 3$ 



**Figure 5:** Bifurcation diagram in the  $M_0M_1 - plane$  when  $M_2 = 11$ 

The two cases  $M_2 < \tilde{M}_2$  and  $M_2 > \tilde{M}_2$  give rise to two qualitatively different bifurcation diagrams, compare Figure 1 with Figures 2-5. In terms of these notations the results in [2] imply: (a)  $P_2$  exists for  $M_1 > f_2(M_0)$  and dim  $W^s(P_2) = i$  in C(i), i = 1, 3. (b) In the region where  $M_1 > f_3(M_0)$ ,  $P_2$  is a source above the NS2-curve and saddle with dim  $W^s(P_2) = 2$  below it.

## **3.3** Preliminary Remarks about *P*<sub>3</sub> and Further Characteristics of the Parameter Space

The fixed point  $P_3$  exists for  $M_0 > e^{1/M_2}(1 + 1/M_1)$ , that is above  $F_3$ . It has the coordinates  $(x_3, u_3, z_3)$ , where

$$u_{3} = 1/M_{2},$$
  

$$z_{3} = \ln(M_{1}(M_{0}e^{-u_{3}} - 1)),$$
  

$$x_{3} = \frac{M_{0}e^{-u_{3}} - 1}{\kappa(u_{3})\kappa(z_{3})},$$

if  $\kappa(u_3)\kappa(z_3) > e^{-u_3}$ . Otherwise  $u_3 = 1/M_2$  but  $z_3$  is the unique solution of

$$\frac{e^{\zeta}}{\kappa(z)}=M_1\kappa(u_3)(M_0-e^{u_3}),$$

and

$$x_3=\frac{e^{x_3}}{M_1\kappa(u_3)\kappa(z_3)}.$$

We will refer to the first case as

**Condition 3.6**  $\kappa(u_3)\kappa(z_3) > e^{-u_3}$ .

The curve determining the boundary between these two cases is of significant importance. We define it as follows:

**Definition 3.7 (Notation**  $F_c$ ) We denote by  $F_c$  the curve  $M_1 = f_c(M_0) = e^{z^*}/(M_0e^{-u_3}-1)$ ,  $M_0 > e^{u_3}$ , where  $z^*$  is the unique solution to  $\kappa(z^*) = e^{-u_3}/\kappa(u_3)$ ,  $u_3 = 1/M_2$ .

It follows that that  $f_c(M_0) > f_3(M_0)$ , so  $P_3$  meets Condition 3.6 for  $M_1 < f_c(M_0)$  whereas it ceases to meet it for  $M_1 > f_c(M_0)$ . Thus, the curve  $F_c$  divides the region above  $F_3$  in  $M_0M_1$ -plane into two parts (cf. Figure 2). We define:

**Definition 3.8 (Notation A, B)** The region between  $F_3$  and  $F_c$  we denote by A and the region above  $F_c$  by *B*.

If  $M_2 > \tilde{M}_2$ , the NS2-curve divides the region A into two subregions:

**Definition 3.9 (Notation**  $A(0, 1), A(2, \star)$ ) If  $M_2 > \tilde{M}_2$ , we denote by A(0, 1) the part above the NS2-curve and the other part by  $A(2, \star)$ .

The numbers alluded to in the above definition, refer to the dimension of the stable manifolds of  $P_2$  and  $P_3$ , respectively. This means that dim  $W^s(P_2) = 0$  in A(0, 1) and dim  $W^s(P_2) = 2$  in  $A(2, \star)$ . We discuss the further subdivisions needed and their relation to the dimension of the stable manifold of  $P_3$  later.

Similarly, the NS2-curve does not always divide the region B into two subregions. Consider the equation:

$$\kappa(u_3)\kappa(u_{max}-u_3)=e^{-u_3}$$

 $(u_{max} \text{ was defined by (7)})$  and let  $u^*$  be its unique solution. From Lemma 5.6 to be formulated in Section 5 follows that  $z_3$  increases in w and tends to  $u_{max} - u_3$  for  $w \to w_{max}$  so the NS2-curve intersects  $F_c$  if and only if  $\kappa(u_3)\kappa(u_{max} - u_3) < e^{u_3}$  which is equivalent to  $u_3 < u^*$ . Now put  $M_2^* = 1/u^* \sim 1.344$ . Our NS2-curve intersects  $F_c$  if  $M_2 > M_2^*$  (Figures 3-5), otherwise it does not (Figures 1-2).

**Definition 3.10 (Notation**  $B(0, 1), B(2, \star)$ ) If  $M_2 > M_2^*$  the NS2-curve divides B into two parts. We call the part above the curve B(0, 1) and the other  $B(2, \star)$ .

We conclude that dim  $W^s(P_2) = 0$  in B(0, 1) and that dim  $W^s(P_2) = 2$  in  $B(2, \star)$ , so the first number to the dimension of the stable manifold of  $P_2$ , whereas the second number refers to the dimension of the stable manifold of  $P_3$ . We summarize the results obtained so far by stating that: We know that  $P_3$  exists in  $A \cup B$ and we know the behavior of  $P_2$  in this region. We continue by examining the bifurcations of  $P_3$ . Its most essential bifurcation is its Neimark-Sacker bifurcation<sup>[2]</sup>. We end this section by introducing

**Definition 3.11 (Notation NS3)** *We call the Neimark-Sacker bifurcation curve for*  $P_3$  *in the*  $M_0M_1$ *-space the* NS3*-curve.* 

## 4. FORMULATION OF THE RESULTS

One of the major objectives with this paper is to relate the location of the NS3-curve to the location of the NS2-curve in the  $M_0M_1$ -parameter space. This is essential for understanding the stability complexity relation of the system (1). Our theorem about the stability-complexity relation in system (1) reads:

**Theorem 4.1 (Stability-complexity theorem)** The NS3-curves are always located in  $A(2, \star) \cup B(2, \star)$ .

This means that the NS3-curve will be located below the NS2-curve and will imply that longer food chains possess less stable dynamics than shorter food chains. Another objective is to exclude the possibility of having strong resonances along the NS3-curves. One such result reads:

#### **Lemma 4.2** (No Fold-Flip Lemma) There are no bifurcations due to eigenvalues $\pm 1$ for $P_3$ in $A \cup B$ .

The proof of this lemma can be found as the last proof in Section 7. That there are no such bifurcations (and also no strong resonances) for  $P_2$  in  $A \cup B \cup C$  was proved by [2]. A similar result for  $P_3$  whenever Condition 3.6 holds was also stated together with a result that excludes strong resonances for large parts of the parameter space as long as Condition 3.6 holds. We subdivide the regions A and B precisely in the next theorem using the results above. The corresponding figures are schematic and not exact, for example, the region B(2, 3) is usually very thin. In all figures the parameter  $M_0$  is at the horizontal axis whereas the parameter  $M_1$  is at the vertical axis.

**Theorem 4.3 (Bifurcation diagram theorem)** The following statements hold:

- (a)  $P_2$  exists in  $A \cup B \cup C$  and  $P_3$  in  $A \cup B$ . We have dim  $W^s(P_2) = i$  in C(i), i = 1, 3,
- (b) If  $M_2 < \tilde{M}_2$ , then dim  $W^s(P_2) = 0$  in  $A \cup B$  and dim  $W^s(P_3) = 1$  in  $A \cup B$  (see Figure 1),
- (c) If M<sub>2</sub> < M<sub>2</sub> < M<sub>2</sub>, then dim W<sup>s</sup>(P<sub>2</sub>) = 0 in A(0, 1) ∪ B, dim W<sup>s</sup>(P<sub>2</sub>) = 2 in A(2, ★), dim W<sup>s</sup>(P<sub>3</sub>) = 1 in A(0, 1) ∪ B. The NS3-curve divides A(2, ★) into two parts A(2, 1) and A(2, 3) so that dim W<sup>s</sup>(P<sub>3</sub>) = i in A(2, i), i = 1, 3 (see Figure 2),
- (d) If  $M_2 > M_2^*$ , then dim  $W^s(P_2) = 0$  in  $A(0, 1) \cup B(0, 1)$ , dim  $W^s(P_2) = 2$  in  $A(2, \star) \cup B(2, \star)$ , dim  $W^s(P_3) = 1$  in  $A(0, 1) \cup B(0, 1)$ , and the NS3-curve divides  $A(2, \star)$  into two parts A(2, 1) and A(2, 3) so that dim  $W^s(P_3) = i$  in A(2, i), i = 1, 3 (see Figure 3 and Figure 4). Sometimes it might also divide B(2) into two parts B(2, 1) and B(2, 3) so that dim  $W^s(P_3) = i$  in B(2, i), i = 1, 3 (see Figure 5).

The theorem follows immediately from the results of Section 3. and the Stability-complexity theorem and No Fold-Flip lemma. The type of the point  $P_2$  in different regions follows from the results of Section 3. From the Stability-complexity theorem and No Fold-Flip theorem follow that the type of  $P_3$  can only change when passing through the NS3-curves which must always be below the NS2-curve and above the  $F_2$ -curve. This means that this curve can only divide the regions A(2, \*) and B(2, \*) into parts. From the results of [2] follow that this point exists above the  $F_2$ -curve and it is stable just above the  $F_2$ -curve for  $M_0 > e^{u_3}$  and unstable for  $M_0 < e^{u_3}$ .

The essential changes in the plane bifurcation diagrams  $(M_0M_1$ -plane) for increasing values of  $M_2$  (after excluding region *E*) may therefore (in the light of Theorem 4.3) be explained as follows: For low values of  $M_2$  (the case  $M_2 = .5$  is illustrated in Figure 1) the  $M_0M_1$ -plane can be divided in five regions: *D* (neither  $P_2$  nor  $P_3$  exist), C(3) ( $P_2$  exists and is stable,  $P_3$  does not exist), C(1) ( $P_2$  exists and is unstable in the *XU*-plane,  $P_3$  does not exist), *A* ( $P_2$  exists and is unstable in all directions,  $P_3$  exists and is stable, Condition 3.6 is satisfied), *B* (Same as *A* but Condition 3.6 is not satisfied) For moderately low values of  $M_2$  (the case  $M_2 = 1$  is illustrated in Figure 2) the region *A* is divided into three regions (in all these cases Condition 3.6 holds): A(2, 3) ( $P_2$  exists and is stable in the *XU*-plane,  $P_3$  exists and is stable), A(2, 1) ( $P_2$  exists and is stable).

As the parameter value  $M_2$  increases, the region *B* splits into two regions B(0, 1) and B(2, 1) (the case  $M_2 = 2$  is illustrated in Figure 3). The emergence of region B(2, 1) allows equilibrium  $P_2$  to be stable in the *XU*-plane together with an unstable equilibrium  $P_3$  that fails to meet Condition 3.6. As the parameter  $M_2$  is further increased (we have illustrated the case  $M_3 = 3$  in Figure 4) the NS3-curve intersects  $F_c$ , but no new region appears. This implies that the equilibrium  $P_3$  may lose its stability by passing the boundary where Condition 3.6 is satisfied. Such parameter values denote examples outside the applicability range of Theorem 4.4 in [2] (low  $M_1$  combined with high  $M_2$  meaning efficient carnivores combined with in-efficient herbivores).

For still higher values of  $M_2$  (we have illustrated the case  $M_2 = 11$  in Figure 4) one narrow region, B(2, 3) between two solid lines appear. This narrow region corresponds to a situation where  $P_3$  is stable and fails meeting Condition 3.6 together with  $P_2$  stable in the XU-plane.

The rest of the paper is organized as follows. In Section 5 we pay attention to the Neimark-Sacker bifurcation of  $P_3$  under Condition 3.6 and prove Theorem 4.1 under this condition. This case refers to Figures 1-3. The case when Condition 3.6 is not satisfied will be considered in Section 6 and refers to Figures 4 and 5. From now on, we divide the analysis of the different bifurcation sequences of system 1 into two parts depending on whether Condition 3.6 is satisfied (Figures 1-3) or not (Figures 4-5) as  $P_3$  loses its stability. We postpone the proofs of a number of lemmas containing, for instance, technical estimates needed in the in the proofs of our results, to Section 7.

*Remarks:* Our Stability-complexity theorem states that the complete food-chain is never more stable than the corresponding plant-herbivore system. This result is a local result but numerical results, for instance, the results in [2], gives reason to believe that if the solutions of the plant-herbivore system are oscillatory, then the oscillations of the corresponding food-chain with a carnivore added must be more violent and the corresponding system is less persistent<sup>[14]</sup>.

## 5. PROOF OF THE STABILITY-COMPLEXITY THEOREM IN REGION A

Under Condition 3.6 the characteristic polynomial  $P(\lambda) = \lambda^3 + \alpha \lambda^2 + \beta \lambda + \gamma$  at  $P_3$  has the coefficients

$$\begin{aligned} \alpha &= \frac{-1 + u_3 - \kappa(z_3)\mathcal{M}^2 x_3 + \mathcal{K} z_3 - 2\mathcal{M} + u_3 \mathcal{M} - \kappa(z_3)\mathcal{M} x_3 + \mathcal{M} \mathcal{K} z_3}{1 + \mathcal{M}}, \\ \beta &= \frac{-1 - u_3 + 2\kappa(z_3)\mathcal{M}^2 x_3 + z_3 + \mathcal{M} - \mathcal{M} u_3 + 2\kappa(z_3)\mathcal{M} x_3 + \mathcal{M} z_3 - \mathcal{M} \mathcal{K} z_3}{1 + \mathcal{M}}, \\ \gamma &= \frac{1 - \kappa(z_3)\mathcal{M} x_3 - \kappa(z_3)\mathcal{M}^2 x_3 - \mathcal{K} z_3 - \mathcal{M} z_3}{1 + \mathcal{M}}, \end{aligned}$$

where

$$\mathcal{M} = M_1 e^{-z_3}$$
 and  $\mathcal{K} = -\frac{\kappa'(z_3)}{\kappa(z_3)}$ . (9)

According to the Schur-Cohn criteria<sup>[15–17]</sup>, a necessary condition for Neimark-Sacker bifurcation is that  $k_{ns} = 0$  when

$$k_{ns} = 1 - \beta - \gamma(\gamma - \alpha). \tag{10}$$

The general idea is to prove that  $k_{ns} < 0$  in A(2). In order to get a Neimark-Sacker bifurcation for  $P_3$  the condition  $k_{ns} = 0$  must be satisfied. Thus, if  $k_{ns}$  does not change sign on the bifurcation curve for  $P_2$  it is always unstable there if it does not satisfy some other bifurcation conditions. It follows from [2] that no other codimension 1 bifurcations are possible.

The Stability-complexity theorem (Theorem 4.1) in Region A follows from four statements labeled below as Propositions 5.1-5.4. To formulate these propositions we introduce a change of coordinates in the region  $A \cup B$  by

$$v = 2 - \frac{1}{\kappa(u_3)} - \frac{e^{u_3}}{M_0}, \ z_3 = \ln(M_1(M_0e^{-u_3} - 1)),$$
 (11)

from  $M_0M_1$ -space to  $vz_3$ -space. Region A corresponds now to the region given by

$$1 - \frac{1}{\kappa(u_3)} < \nu < 2 - \frac{1}{\kappa(u_3)}$$
 and  $0 < z_3 < z^*$ ,

where  $z^*$  is the solution to  $\kappa(u_3)\kappa(z_3) = e^{-u_3}$ .

We introduce the notation

$$\mathcal{A}(u_3) = 2 - \frac{1}{\kappa(u_3)}.$$
(12)

This function occurs frequently in proofs of the subsequent statements. Note that  $\mathcal{A}$  decreases for  $u_3 \ge 0$  ( $\kappa$  has the same property), that  $\mathcal{A}(0) = 1$ , and that  $\mathcal{A}(u_{max}) = 0$  follows from (8). We shall suppress the argument of this function. The inequality  $\mathcal{A} - 1 < v < \mathcal{A}$  is satisfied in Region A.

We now formulate the above mentioned statements.

**Proposition 5.1** Under Condition 3.6,  $z_3 > v$  on the NS2-curve (5) for  $u_3 < u_{max}$ .

**Proposition 5.2** Under Condition 3.6,  $k_{ns} < 0$  for  $z_3 > v$ ,  $0 < v < \mathcal{A}$  and  $u_3 < u_{max}$ .

**Proposition 5.3** There is no Neimark-Sacker bifurcation for  $v \le 0$  and positive  $z_3$  and  $u_3 < u_{max}$ .

**Proposition 5.4** There is no Neimark-Sacker bifurcation for  $P_3$  for  $M_2 < \tilde{M}_2 < M_2^*$ .

We now show that Theorem 4.1 follows from the propositions above.

**Proof of Theorem 4.1:** We first prove that there is no Neimark-Sacker bifurcation for  $P_3$  in A(0, 1). Let us consider the case  $u_3 < u_{max}$  (cf. (7)). According to Proposition 5.2 the NS3-curve cannot be in the region  $z_3 > v$  for positive v. But according to Proposition 5.1, the NS2-curve must be there. Similarly, according to Proposition 5.3 there is no Neimark-Sacker bifurcation for negative v. Thus, in this case the NS3-curve must be in  $A(2, \star)$ . In the case  $u_3 > u_{max}$  it follows from Proposition 5.4 that there are no Neimark-Sacker bifurcations at all in A.  $\Box$ 

We now go on proving Propositions 5.1-5.4 one by one. We formulate some general lemmas and fix notation that is going to be used subsequently.

**Lemma 5.5**  $\mathcal{K} = -\kappa'(z)/\kappa(z)$  is a decreasing function in z for z > 0 and

$$\lim_{z\to 0_+} \mathcal{K} = \frac{1}{2}, \quad \mathcal{K}(u_{max}) = 1 - \frac{1}{u_{max}} \quad and \quad \mathcal{K} > 0,$$

for any positive z.

We define the functions  $\mathcal{B}$  and  $\eta$  according to

$$\mathcal{B}(u_3) = 1 - \mathcal{A}(u_3), \quad \eta(w, u_3) = h(w) - 1 - \mathcal{B}(u_3).$$

Remember that *h* was defined through (4) and note that  $\eta(u_3)$  is closely related to it. The function  $\mathcal{A}$  was introduced through (12). It follows from Lemma 3.3 that  $\eta$  is an increasing function in *w*. Substitution of relevant arguments in the formulas shows that  $\eta(e^{u_3}, u_3) = 0$  and  $\eta(w_{max}, u_3) = \mathcal{A}(u_3)$ . We are going to suppress the arguments of the functions defined above.

We next reparametrize the expressions for  $z_3$  and v given by (11) on the NS2-curve (5) as functions of  $\rho = we^{-u_3} - 1$ . Calculations give

$$z_3 = \ln\left(\frac{\rho}{\eta + \mathcal{B}} + 1\right), \quad \nu = \frac{\eta + \mathcal{A}\rho}{\rho + 1}.$$
(13)

The functions  $z_3$  and  $\nu$  are defined for  $0 < \rho < \rho_{max} = w_{max}e^{-u_3} - 1$  and the idea of the reparametrization is that the parameter should start from zero instead of  $e^{u_3}$ . We continue formulating lemmas concerning the properties of the newly defined functions. In fact, Lemmas 5.8 and 5.9 give important estimates for the function  $\eta$ .

**Lemma 5.6**  $z_3$  is an increasing function in  $\rho$  for  $\rho \in [0, \rho_{max}]$  where  $\rho_{max} = w_{max}e^{-u_3} - 1$  and  $\lim_{\rho \to 0_+} z_3 = 0$ and  $z_3(\rho_{max}) = u_{max} - u_3$ .

**Lemma 5.7** *v* is an increasing function in  $\rho$  for  $\rho = [0, \rho_{max}]$  and v(0) = 0 and  $v(\rho_{max}) = \mathcal{A}$ .

**Lemma 5.8** If  $w = (\rho + 1)e^{u_3}$  then  $\sigma = \eta/\rho < s$  for  $\rho > 0$ , where s is the derivative of  $\eta$  with respect to  $\rho$  taken at  $\rho = 0$ .

**Lemma 5.9** The functions  $\sigma$  and s in Lemma 5.8 are increasing in  $u_3$  and  $\sigma$  is decreasing in  $\rho$ . Moreover, 1/2 < s < 3/4 for  $0 < u_3 < u_{max}$ .

Proofs of lemmas are as usual given in Section 7. To prove Proposition 5.1 we finally need Lemma 5.10 estimating the logarithmic function from below with one of its Padé approximations<sup>[7]</sup>.

**Lemma 5.10**  $\ln(t+1) > 2t/(t+2)$  for t > 0.

Proof of Proposition 5.1: Lemma 5.8 and Lemma 5.10 give

$$z_3 = \ln\left(\frac{\rho}{\eta + \mathcal{B}} + 1\right) > \frac{2\rho}{\rho + 2(\eta + \mathcal{B})} = \frac{2\rho}{\rho + 2(\sigma\rho + \mathcal{B})}.$$

Using notation in Lemma 5.8, we get

$$\nu = \frac{\eta + \mathcal{A}\rho}{\rho + 1} = \frac{(\sigma + \mathcal{A})\rho}{\rho + 1}.$$

Thus, we wish to prove

$$\frac{2\rho}{\rho+2(\sigma\rho+1-\mathcal{A})} > \frac{(\sigma+\mathcal{A})\rho}{\rho+1},\tag{14}$$

which is equivalent to prove  $q_1 \rho < 2q_2$ , where  $q_1 = 2\sigma^2 + (2\mathcal{A} + 1)\sigma + \mathcal{A} - 2$  and  $q_2 = \mathcal{A}^2 + (1 - \sigma)(1 - \mathcal{A})$ . It follows from the properties of  $\mathcal{A}$  that  $0 \le \mathcal{A} < 1$  and from Lemma 5.9 follows  $\sigma < 3/4$  implying  $q_2 > 0$ . Thus, (14) holds if  $q_1 \le 0$  and we further consider only the case when  $q_1 > 0$ . Then (14) is equivalent to  $\rho < 2q_2/q_1 = q$ . *q* is decreasing in  $\sigma$  because  $q_2$  is decreasing and  $q_1$  increasing in  $\sigma$ . So *q* is always greater than the value it takes for greatest  $\sigma$  which is taken for lowest  $\rho$  and greatest  $u_3$ . The sign of the derivative of *q* with respect to *A* is determined by a second order polynomial. The minimum of *q* is taken at the root of the derivative if this root is less than 1 and is inside the interval where *q* is positive. Otherwise it is taken at A = 1. Because  $\sigma < 3/4$  according to Lemma 5.9 we can use this value for estimating *q* getting q > 0.65. Thus, inequality (14) holds for  $\rho \le 0.65$ . Because  $\rho < \rho_{max} = w_{max}e^{-u_3} - 1$  we get  $u_3 < u_{max} - \ln(1.65)$  for  $\rho > 0.65$ . Using this  $u_3$ -value and  $\rho = 0.65$  we estimate  $\sigma < 0.548$ . Using this  $\sigma$  in the same estimating procedure as above we find that inequality (14) is valid for  $0.65 < \rho \le 1.6$ . Repeating this estimation procedure we find that inequality (14) is valid for all  $\rho < \rho_{max}$  and thus,  $z_3 > v$ .

Now, since the used expressions for  $z_3$  and v (13) were evaluated at the NS2-curve (5), Proposition 5.1 follows.  $\Box$ 

In the proof of the next proposition, we need to consider the expression

$$P = \kappa(u_3)k^2\nu^2 + (2k\kappa(u_3) + k^2)\nu + \kappa(u_3)u_3k + \kappa(u_3), \quad k = \mathcal{K} - 1,$$

which is factor in (10) for  $z_3 = v$ . The first part of the proof of Proposition 5.2 is actually based on the following lemma:

**Lemma 5.11** *P* is positive for  $0 < u_3 \le u_{max}$  and  $0 < v \le \mathcal{A} = 2 - 1/\kappa(u_3)$ .

**Proof of Proposition 5.2:** We need to calculate the expression for  $k_{ns}$  as a function of v and  $z_3$ . We get

$$k_{ns} = \frac{q_{22}z_3^2 v^2 + q_{12}z_3^2 v + q_{02}z_3^2 + q_{21}z_3 v^2 + q_{11}z_3 v + q_{01}z_3 + q_{10}v}{\kappa(u_3)^2},$$

where

$$\begin{split} q_{22} &= -\kappa(u_3)^2 k^2, \\ q_{12} &= k\kappa(u_3)(k\kappa(u_3) - 3\kappa(u_3) - 2k), \\ q_{02} &= (2\kappa(u_3) + k)(-k + k\kappa(u_3) - \kappa(u_3)), \\ q_{21} &= \kappa(u_3)^2 k, \\ q_{11} &= -\kappa(u_3)(\kappa(u_3)u_3k - \kappa(u_3) - k), \\ q_{01} &= \kappa(u_3)(\kappa(u_3) + \kappa(u_3)u_3k - u_3\kappa(u_3) - u_3k - 1), \\ q_{10} &= u_3\kappa(u_3)^2, \end{split}$$

and  $\mu = M + 1$  and k = K - 1. We notice that k depends on z, but it is very little varying and these properties are given by Lemma 5.5. Again, we split the proof into two parts.

(a) The first part reads: Under Condition 3.6,  $k_{ns} < 0$  for  $z_3 = v$ ,  $0 < v < \mathcal{A}$ .

The numerator determining the sign of  $k_{ns}$  becomes  $-(\nu\kappa(u_3) + 1 - \kappa(u_3))P\nu$  for  $z_3 = \nu$ . From Lemma 5.11 follows P > 0 for  $0 < u_3 < u_{max}$  and because  $\nu\kappa(u_3) + 1 - \kappa(u_3) > 0$  we get  $k_{ns} < 0$ .

(b) The second part we are going to prove states that: Under Condition 3.6,  $k_{ns} < 0$  for  $z_3 = v$ ,  $0 < v < \mathcal{A}$  implies  $k_{ns} < 0$  for  $z_3 > v$ ,  $0 < v < \mathcal{A}$ .

The statement (b) simply says that statement (a) implies Proposition 5.2 and is easier to prove than (a). We now prove (b). We make the change of variable  $\zeta = z_3 - \nu$  so that  $z_3 > \nu$  means  $\zeta > 0$ . The numerator of  $k_{ns}$  takes the form  $q_{n2}\zeta^2 + q_{n1}\zeta + q_{n0}$  where

$$q_{n2} = -(\nu \kappa(u_3)k + k + 2\kappa(u_3))(\nu \kappa(u_3)k + k + \kappa(u_3) - k\kappa(u_3)),$$

 $q_{n0}$  is the expression proved negative in the proof of (a) and

$$q_{n1} = q_{n11} + q_{n12} + q_{n13}u + q_{n14}v^2 + q_{n15}v,$$

where

$$\begin{split} q_{n11} &= -2\kappa(u_3)^2\nu(\nu k+1)^2 < 0, \\ q_{n12} &= (\kappa(u_3)^2 - \kappa(u_3))(2\nu k+1)^2 < 0, \\ q_{n13} &= (\kappa(u_3)^2 - \kappa(u_3) - \nu\kappa(u_3)^2)k - \kappa(u_3)^2, \\ q_{n14} &= -\kappa(u_3)^2(2k^2 + k), \\ q_{n15} &= 2(\kappa(u_3) - 1)k^2 - k\kappa(u_3) - \kappa(u_3)^2. \end{split}$$

We first analyze  $q_{n2}$ . Since k < 0 the smallest value of  $\nu \kappa(u_3)k + k + 2\kappa(u_3)$  is taken for  $\nu = 2 - 1/\kappa(u_3)$ . It is  $2\kappa(u_3)\mathcal{K} > 0$ . The smallest value of  $\nu \kappa(u_3)k + k + \kappa(u_3) - k\kappa(u_3)$ ) is taken for the same  $\nu$  and it is  $\kappa(u_3)\mathcal{K} > 0$ . Thus,  $q_{n2} < 0$ . We finally analyze  $q_{n1}$ .  $q_{n13}$  is maximal for the maximal value of  $\nu$  and thus, substituting  $\nu = \mathcal{A}$  gives  $q_{n13} < -\kappa(u_3)^2 \mathcal{K} < 0$ .  $q_{n14} < 0$  as k < -1/2. Finally by standard finding of global maximum it can be counted that the maximum of  $q_{n15}$  in the region  $-1 \le k < 0$ ,  $1/2 < \kappa(u_3) \le 1$  is zero taken for k = -1 and  $\kappa(u_3) = 1$ . We conclude that  $q_{n1} < 0$ .

Thus,  $q_{n2}$ ,  $q_{n1}$ ,  $q_{n0} < 0$  and  $k_{ns} < 0$  for  $z_3 > v$  and (b) follows.

As earlier mentioned, Proposition 5.2 follows from Statements (a) and (b) above.  $\Box$ 

**Proof of Proposition 5.3:** We prove that  $k_{ns} < 0$  in the case  $v \le 0$  and  $u < u_{max}$ . We do this by looking at the sign of the coefficients  $q_{ij}$  and using that in this case -1 < k < 0 and  $\kappa(u_3) > 1/2$ . It is clear that  $k_{ns} < 0$  if  $q_{22}$ ,  $q_{02}$ ,  $q_{21}$ ,  $q_{01} < 0$  and  $q_{12}$ ,  $q_{11}$ ,  $q_{10} > 0$  and we immediately see that  $q_{22}$ ,  $q_{21} < 0$  and  $q_{10} > 0$ . For  $q_{12}$  we get  $k\kappa(u_3) - 3\kappa(u_3) - 2k < (k-3)/2 - 2k = -3(1+k)/2 < 0$  and thus,  $q_{12} > 0$ . For  $q_{02}$  we get  $2\kappa(u_3) + k > 1 + k > 0$  and  $k\kappa(u_3) - \kappa(u_3) - k = (k-1)\kappa(u_3) - k < (k-1)/2 - k = -(1+k)/2 < 0$  and thus,  $q_{02} < 0$ . For  $q_{11}$  we get  $\kappa(u_3)u_3k - \kappa(u_3) - k = -e^{-u_3}k - \kappa(u_3) < 0$  and thus,  $q_{11} > 0$ . For  $q_{01}$  we get  $q_{01}/\kappa(u_3) = \kappa(u_3) + \kappa(u_3)u_3k - u_3\kappa(u_3) - u_3k - 1 = k(u_3\kappa(u_3) - u_3) - u_3\kappa(u_3) + (\kappa(u_3) - 1)$ . From k > -1 and  $u_3\kappa(u_3) - u_3 < 0$  follows  $q_{01}/\kappa(u_3) < u_3(1 - 2\kappa(u_3)) + (\kappa(u_3) - 1) < 0$  because  $1/2 < \kappa(u_3) < 1$ . Thus,  $q_{01} < 0$  and we have proved that  $k_{ns} < 0$  in this case.  $\Box$ 

**Proof of Proposition 5.4:** We notice that for  $M_2 < \tilde{M}_2$  we get  $u_3 > u_{max}$  and  $0 < \kappa(u_3) < 1/2$ .

A necessary condition for Neimark-Sacker bifurcation as Condition 3.6 holds was that

$$Q_k = k_{ns}\kappa(u_3)^2 = 0.$$

Observe that always  $\nu < \mathcal{A}$  because  $\nu = \mathcal{A} - e^{u_3}/M_0$ . Substituting  $\nu = \nu + \mathcal{A}$  into  $Q_k$  we get

$$Q_k = \kappa(u_3)(q_2 z_3^2 + q_1 z_3 + q_0),$$

where

$$\begin{aligned} q_2 &= -\kappa(u_3)k^2v^2 - 3\kappa(u_3)(k^2 + k)v - 2\kappa(u_3)(1 + k)^2, \\ q_1 &= \kappa(u_3)kv^2 + (((4 - u_3)\kappa(u_3) - 1)k + \kappa(u_3))v + ((-u_3k - u_3 + 3 + 4k)\kappa(u_3) - 2 - 2k) \\ q_0 &= u_3(2\kappa(u_3) - 1) + vu_3\kappa(u_3). \end{aligned}$$

Observing that -1 < k < -1/2 and  $\nu < 0$  we see that  $q_2 < 0$ . Let us now consider  $q_1$ . The coefficient of first order for  $\nu$  is equal to  $(4\kappa(u_3) - 2 + e^{-u_3})k + \kappa(u_3)$  and is linear in k. For k = -1 we get

$$-3\kappa(u_3) - e^{-u_3} + 2 > 2 - \frac{3}{2} - e^{-u_{max}} > \frac{1}{2} - e^{-1} > 0,$$

and for k = 0 we get  $\kappa(u_3) > 0$ . We conclude that the coefficient is positive and because  $\nu < 0$  the middle term in  $q_1$  is negative for  $u > u_{max}$ . The expression  $(-u_3k - u_3 + 3 + 4k)\kappa(u_3) - 2 - 2k$  is linear in  $\kappa(u_3)$  and for  $\kappa(u_3) = 1/2$  it attains the value  $-(u_3k + u_3 + 1)/2 < 0$  and for  $\kappa(u_3) = 0$  the value -2 - 2k < 0 and we conclude that the expression is always negative. The  $\nu^2$ -term is always negative and thus,  $q_1 < 0$ . Finally we find that  $q_0 = u_3(2\kappa(u_3) - 1) + \nu u_3\kappa(u_3) < 0$  because  $\kappa(u_3) < 1/2$  for  $u_3 > u_{max}$ . Consequently  $Q_k < 0$  for  $u_3 > u_{max}$  and in this case there are no Neimark-Sacker bifurcations.  $\Box$ 

# 6. PROOF OF THE STABILITY-COMPLEXITY THEOREM IN REGION *B*

In this section we assume Condition 3.6 is not satisfied. In this case the Jacobian matrix at  $P_3$  takes the form

**1** - 1/2

$$\begin{pmatrix} 1/m & -x_3/m & 0\\ u_3/x_3 & 1/\kappa(u_3) - u_3 - \mathcal{K}z_3 & -u_3 - \mathcal{K}u_3\\ 0 & z_3/u_3 & 1 \end{pmatrix},$$

where

$$m = M_0 e^{-u_3}.$$
 (15)

Computation of the coefficients of the characteristic polynomial gives in this case

$$\alpha = -1 - \frac{1}{\kappa(u_3)} - \frac{1}{m} + u_3 + \mathcal{K}_{Z_3},\tag{16}$$

$$\beta = \frac{1}{\kappa(u_3)} + \frac{1}{m} + \frac{1}{m\kappa(u_3)} - u_3 + z_3 - \frac{\mathcal{K}z_3}{m},\tag{17}$$

$$\gamma = -\frac{1}{m\kappa(u_3)} - \frac{z_3}{m}.$$
(18)

Thus, a necessary criterion on the coefficients for Neimark-Sacker bifurcation reads  $k_{ns} = \frac{Q}{m^2 \kappa (u_3)^2} = 0$ , where

$$Q = q_{12}z_3^2m + q_{02}z_3^2 + q_{21}z_3m^2 + q_{11}z_3m + q_{01}z_3 + q_{20}m^2 + q_{10}m + q_{00},$$

and

$$\begin{aligned} q_{12} &= -\kappa(u_3)^2 \mathcal{K}, \\ q_{02} &= -\kappa(u_3)^2, \\ q_{21} &= -\kappa(u_3)^2, \\ q_{11} &= -\kappa(u_3)(-1 + u_3\kappa(u_3) - \kappa(u_3) + \mathcal{K}(1 - \kappa(u_3))), \\ q_{01} &= \kappa(u_3)(\kappa(u_3) - 2), \\ q_{20} &= \kappa(u_3)(-1 + u_3\kappa(u_3) + \kappa(u_3)), \\ q_{10} &= -u_3\kappa(u_3) + 1 - \kappa(u_3)^2, \\ q_{00} &= -1 + \kappa(u_3). \end{aligned}$$

There is also a one-to-one change of coordinates in B given by (15) and

$$\frac{e^{z_3}}{\kappa(z_3)} = \kappa(u_3)(M_0 - e^{u_3})M_1,$$

from the  $M_0M_1$  space to the *mz*<sub>3</sub>-space and *B* is then given by m > 1 and  $z_3 > z^*$  where  $z^*$  is the unique solution to  $\kappa(z_3) = e^{-u_3}/\kappa(u_3)$ . So we examine  $k_{ns}$  as a function of *m* and  $z_3$ .

The sign of  $k_{ns}$  is determined by the sign of Q and we wish to prove that Q < 0 on the NS2-curve. We split the proof of the stability-complexity theorem (Theorem 4.1) in this case into three major propositions. Note that the conclusion of the first of them holds outside the NS2-curve, too.

**Proposition 6.1** Q < 0 for  $\tilde{M}_2 < M_2 < 5$  and  $u_3 < u_{max}$ .

**Proposition 6.2** Q < 0 for  $M_2 \ge 5$  and  $u_3 < u_{max}$  on the NS2-curve (5).

**Proposition 6.3** There is no Neimark-Sacker bifurcation for  $P_3$  for  $M_2 < \tilde{M}_2$  and  $u_3 > u_{max}$  when Condition 3.6 is not satisfied.

Taken together, these three propositions imply the Stability complexity theorem (Theorem 4.1) in Region B. We go on formulating some lemmas needed in the proof of the propositions above.

**Lemma 6.4**  $\kappa(t)^2 > e^{-t}$  for t > 0.

**Lemma 6.5** If Condition 3.6 is not satisfied, then  $z_3 > u_3$ .

**Lemma 6.6** Let  $q_{-} = 1/\kappa(u_3) - u_3$ . Then  $0 < q_{-} < 1$  and  $q_{-}$  is a decreasing function in  $u_3$  for  $u_3 > 0$ .

**Lemma 6.7** The derivative of Q with respect to  $z_3$  is negative for positive  $z_3$ .

We now use the lemmas above to prove Proposition 6.1.

**Proof of Proposition 6.1:** For  $z_3 = u_3$  we get  $Q = Q_u = A_q m^2 + B_q m + C_q$ , where

$$A_q = -(1-a)a, \quad B_q = (1-a)((1+q)a+qb), \quad C_q = -(b+1)(a+b),$$

and  $a = 1 - \kappa(u_3)$ ,  $b = u_3\kappa(u_3)$  and  $q = 1/\kappa(u_3) - (1 + \mathcal{K})u_3$ .

The only positive coefficient in  $Q_u$  is  $B_q$  and it is greatest for greatest q. Thus, using Lemma 5.5 we get  $Q_u < Q_{u-}$ , where  $Q_{u-}$  is  $Q_u$  for  $\mathcal{K} = 0$ , that is  $Q_{u-} = A_q m^2 + B_- m + C_q$ , where  $B_- = (1-a)((1+q_-)a+q_-b)$ .

Because  $A_q, C_q < 0$  we have  $Q_{u-} < 0$  for any m if  $4A_qC_q > B_-^2$ . Because 0 < a < 1 this is equivalent to

$$\frac{4A_qC_q - B_-^2}{1 - a} = k_Q = q_2b^2 + q_1b + q_0 > 0,$$

where  $q_2 = (4 + q_-^2)a - q_-^2$ ,  $q_1 = a^2(4 + 2q_- + 2q_-^2) + a(4 - 2q_- - 2q_-^2)$  and  $q_0 = a^2(3 - 2q_- - q_-^2) + (1 + q_-)^2a^3$ .

Thus,  $k_Q$  is a second order polynomial in *b*. All the coefficients are increasing with *a* for  $0 < q_- < 1$ . Because  $B_-$  is decreasing with decreasing  $q_-$  the polynomial  $k_Q$  will always be greater than the value it takes for greatest  $q_-$  and smallest *a*. But the greatest  $q_-$  and smallest *a* we get for smallest  $u_3$ . For  $u_3 = 0.4$  all the coefficients  $q_0$ ,  $q_1$  and  $q_2$  are positive and because b > 0 we conclude that  $k_Q > 0$  and thus,  $k_Q > 0$  for  $u_3 \ge 0.4$ . Let us consider the case  $0.2 \le u_3 < 0.4$ . In this case  $k_Q$  is greater than the polynomial  $k'_Q$  where the coefficients  $q_0$ ,  $q_1$  and  $q_2$  are calculated for  $u_3 = 0.2$ . *b* is increasing in  $u_3$  and thus, for  $u_3 < 0.4$  we get  $0 < b < b_+$  where  $b_+$  is the value *b* takes for  $u_3 = 0.4$ . Calculations show that in this *b*-interval  $k'_Q > 0$  and thus, also  $k_Q > 0$ . Consequently  $k_Q > 0$  and Q < 0 for  $u_3 > 0.2$  which is equivalent to  $M_2 > 5$ . From Lemma 6.7 follows that  $Q_u < 0$  for  $z_3 > u_3$  which is always true according to Lemma 6.5.  $\Box$ 

Our numerical investigations of expression  $Q_u$  actually indicate Proposition 6.1 to be true in the range  $M_2 < 10.8$ .

We next split Proposition 6.2 into two sub-propositions. To formulate them we need the following definition.

**Definition 6.8 (Notation S)** The region S in the positive mz-plane is the union of three regions  $S_a$ ,  $S_b$  and  $S_c$ , where

•  $S_a$  is defined by  $0 < m < 1/\kappa(u_3)$  and  $z_3 > 0$ ,

- $S_b$  is defined by  $m \ge 1/\kappa(u_3)$  and  $z_3 > m 1/\kappa(u_3)$  and
- $S_c$  is defined by  $z_3 > 0.25$  and m > 0.

We now formulate the above mentioned two sub-propositions.

**Proposition 6.9** Q < 0 in *S* for  $0 < u_3 \le 0.2$ .

**Proposition 6.10**  $(z, m) \in S$  on the NS2-curve for  $0 < u_3 \le 0.2$ .

We see that the first one guarantees Q to be negative in S for  $M_2 \ge 5$ . The second guarantees that the NS2-curve is located inside S for  $M_2 \ge 5$ , so provided these sub-propositions can be proved, Proposition 6.2 follows. Before we go on proving Proposition 6.9 we formulate one lemma.

Lemma 6.11 If Condition 3.6 is not satisfied then

$$\frac{2}{3}\ln(\kappa(u_3)e^{u_3}) + \frac{2}{3}\ln(M_1(M_0e^{-u_3} - 1)) < z_3 < \ln(M_1(M_0e^{-u_3} - 1)),$$

and on the NS2-curve (5)

$$\ln(M_1(M_0e^{-u_3}-1)) = \ln(\frac{\rho}{g}+1), \quad g = h - 1,$$

 $z_3$  is increasing with w on the NS2-curve (5).

**Proof of Proposition 6.9:** We prove that the Proposition holds in each of the subregions  $S_a$ ,  $S_b$  and  $S_c$  corresponding to parts (a), (b), and (c) below.

(a) We start by proving that Q < 0 in  $S_a$ .

For  $z_3 = 0$  we get  $Q = Q_0$  which is a second order polynomial in *m* and negative for  $0 < m < 1/\kappa(u_3)$  (the roots of  $Q_0$  are  $1/\kappa(u_3)$  and  $(\kappa(u_3) - 1)/(\kappa(u_3) - e^{-u_3}) < 0$ , the coefficient for  $m^2$  is positive). From Lemma 6.7 we conclude that Q < 0 for  $z_3 > 0$  and  $0 < m < 1/\kappa(u_3)$ .

(b) We continue by proving that Q < 0 in  $S_b$ .

Let  $Q_z$  be the expression obtained from Q by substituting  $z_3 = m - 1/\kappa(u_3)$ . If we make the substitution  $m = m_k + 1/\kappa(u_3)$  and divide  $Q_z$  by  $m_k m \kappa(u_3)$  we get

$$\frac{Q_z}{m_k m \kappa(u_3)} = -(\mathcal{K}+1)(\kappa(u_3)m_k + 1 - \kappa(u_3)) < 0,$$

for  $m_k$  positive. Thus, Q < 0 for  $z_3 = m - 1/\kappa(u_3)$ . Again from Lemma 6.7 we conclude that Q < 0 for  $z_3 > m - 1/\kappa(u_3)$  and  $m > 1/\kappa(u_3)$ .

(c) The last part is to prove that Q < 0 in  $S_c$ .

For the coefficients of Q we get the following estimates:

 $\begin{aligned} q_{10} &= e^{-u_3} - \kappa(u_3)^2 < 0 \text{ (follows from Lemma 6.4),} \\ q_{12} &< 0, q_{01}/\kappa(u_3) < -1, \\ q_{11}/\kappa(u_3) &< e^{-u_3} + \kappa(u_3) - \mathcal{K}(1 - \kappa(u_3)) < 2\kappa(u_3) \text{ (because } 1 - u_3\kappa(u_3) = e^{-u_3} < \kappa(u_3) \text{ and } \mathcal{K} > 0), \\ q_{20}/\kappa(u_3) &= c, \ q_{21} = q_{02} = -\kappa(u_3)^2, \ c &= \kappa(u_3) - e^{-u_3} > 0. \end{aligned}$ 

Using these estimates we get

$$\frac{Q}{\kappa(u_3)} < m^2(c - \kappa(u_3)z_3) + 2\kappa(u_3)z_3m - z_3 - \kappa(u_3)z_3^2 - \frac{1 - \kappa(u_3)}{\kappa(u_3)} = Q_1.$$

Considering  $Q_1$  as a second order polynomial in *m* we conclude that Q < 0 for any *m* if

$$4(\kappa(u_3)z_3-c)\left(z_3+\kappa(u_3)z_3^2+\frac{1-\kappa(u_3)}{\kappa(u_3)}\right)>4\kappa(u_3)^2z_3^2,$$

which is equivalent to

$$Q_k = \kappa(u_3)^2 z_3^3 + \kappa(u_3)(1 - c - \kappa(u_3))z_3^2 + (1 - \kappa(u_3) - c)z_3 - \frac{(1 - \kappa(u_3))c}{\kappa(u_3)} > 0.$$

Because  $\kappa(u_3) < 1 - u_3/2 + u_3^2/6$  and  $e^{-u_3} > 1 - u_3 + u_3^2/2 - u_3^3/6$ , we get

$$1 - c - \kappa(u_3) = 1 + e^{-u_3} - 2\kappa(u_3) > (u_3^2 - u_3^3)/6 > 0,$$

for  $u_3 < 1$  and thus, the coefficients for  $z_3^2$  and  $z_3$  are positive. Consequently we get

$$Q_k > \kappa(u_3)^2 z_3^3 - \frac{(1 - \kappa(u_3))c}{\kappa(u_3)}.$$

Thus,  $Q_k > 0$  if

$$z_3 > z_- = \left(\frac{(1 - \kappa(u_3))c}{\kappa(u_3)^3}\right)^{1/3}$$

We notice that  $(1 - \kappa(u_3))c/\kappa(u_3)$  increases with  $u_3$  while the coefficient for  $z_3^3$  decreases with  $u_3$ .

We now prove that *c* increases with  $u_3$  for small  $u_3$  by checking the sign of the derivative with respect to  $u_3$ . We get

$$c' = \frac{(1+u_3+u_3^2)e^{-u_3}-1}{u_3^2} > 1/2 - 2u_3/3 + u_3^2/3 - u_3^3/6,$$

and c' > 0 for  $0 < u_3 < 1$ . Thus, because  $\kappa(u_3)$  is decreasing in  $u_3$  the value of  $z_-$  is less or equal to the value it gets for  $u_3 = 0.2$  which is less than 0.25.  $\Box$ 

We proceed by proving Proposition 6.10, also this proof splits into three main parts.

#### **Proof of Proposition 6.10:**

(a) We first prove that  $z_3 - \frac{2}{3} \ln(\kappa(u_3)e^{u_3}) > m - \frac{1}{\mathcal{A}}$  for  $\rho = we^{-u_3} - 1 < 0.1$  and  $0 < u_3 \le 0.2$  on the NS2-curve (5).

From Lemmas 6.11, 5.10, and 5.8 follow that

$$z_3 - \frac{2}{3}\ln(\kappa(u_3)e^{u_3}) > \frac{4}{3}\frac{\rho}{\rho + 2g} > \frac{4\rho}{3(\rho + 2s\rho + 2\mathcal{B})}$$

where  $\mathcal{B} = 1 - \mathcal{A}$ . Calculations and Lemma 5.8 give

$$m - \frac{1}{\mathcal{A}} = \frac{we^{-u_3}}{1-g} - \frac{1}{\mathcal{A}} = \frac{\mathcal{A}\rho + \eta}{\mathcal{A}(1-g)} < \frac{(\mathcal{A}+s)\rho}{\mathcal{A}(1-s\rho - \mathcal{B})}$$

Consequently  $z_3 - \frac{2}{3} \ln(\kappa(u_3)e^{u_3}) > m - 1/\mathcal{A}$  if the inequality

$$\frac{4}{3((1+2s)\rho+2\mathcal{B})} > \frac{\mathcal{A}+s}{\mathcal{A}(1-s\rho-\mathcal{B})}$$

is satisfied. This inequality is equivalent to

$$\rho < \frac{10\mathcal{A}^2 - 6\mathcal{A} - 6s + 6\mathcal{A}s}{3\mathcal{A} + 3s + 10\mathcal{A}s + 6s^2} = \rho_1.$$

The smallest value of  $\rho_1$  for varying s is taken for greatest s < 3/4. So

$$\rho_1 > \frac{4(20\mathcal{A}^2 - 3\mathcal{A} - 9)}{3(28\mathcal{A} + 15)} = \rho_2.$$

 $\rho_2$  is increasing for increasing  $\mathcal{A}$  if  $\mathcal{A} > 0$  (the derivative of  $\rho_2$  with respect to  $\mathcal{A}$  is positive for positive  $\mathcal{A}$ ). Thus,  $\rho_2$  is greater than the value it takes for smallest  $\mathcal{A}$ . Smallest  $\mathcal{A} > 0.896$  is taken for  $u_3 = 0.2$ . For this  $\mathcal{A}$  we get  $\rho_2 > 0.1$ 

(b) The next part is to show that  $z_3 - \frac{2}{3} \ln(\kappa(u_3)e^{u_3}) > 0.25$  for  $\rho = 0.1$  on the NS2-curve (5) when  $u_3$  satisfies the condition:  $0 < u_3 \le 0.2$ .

As in the previous part of this proof we get

$$z_3 - \frac{2}{3}\ln(\kappa(u_3)e^{u_3}) > \frac{4\rho}{3(\rho + 2g)} > \frac{4\rho}{3((1+2s)\rho + 2\mathcal{B})} = z_1$$

But the smallest value of  $z_1$  is taken for for greatest s < 3/4 and  $\mathcal{B}$  and smallest  $\mathcal{A}$ . For  $u_3 \le 0.2$  we get  $\mathcal{A} > 0.896$ . Evaluating  $z_1$  for s = 3/4 and  $\mathcal{A} = 0.896$  we get  $z_1 > 0.25$  for  $\rho = 0.1$ .

(c) The last part is to prove that  $\frac{2}{3} \ln(\kappa(u_3)e^{u_3}) > 1/\mathcal{A} - 1/\kappa(u_3)$  for  $0 < u_3 < 0.475$ .

Using  $\kappa(u_3)e^{u_3} = (e^{u_3} - 1)/u_3 > 1 + u_3/2$  and Lemma 5.10 we get

$$\frac{2}{3}\ln(\kappa(u_3)e^{u_3}) > \frac{2}{3}\ln(1+u_3/2) > \frac{4}{3}\frac{u_3}{u_3+4}$$

Calculations give  $1/\mathcal{A} - 1/\kappa(u_3) = (x-1)^2(2-x)^{-1}$ , where  $x = 1/\kappa(u_3)$ . This expression is increasing with x and  $x < 1/(1-u_3/2) = 2/(2-u_3)$ . Thus,

$$\frac{(x-1)^2}{2-x} < \frac{\left(\frac{2}{2-u_3}-1\right)^2}{2-\frac{2}{2-u_3}} = \frac{u_3^2}{(2-u_3)(2-2u_3)}$$

But  $u_3^2/((2 - u_3)(2 - 2u_3)) < 4u_3/(3(u_3 + 4))$  is for  $0 < u_3 < 1$  equivalent to the inequality

$$5u_3^2 - 36u_3 + 16 > 0,$$

which is seen to hold for  $0 < u_3 < 0.475$ .

We conclude that Proposition 6.10 holds since, from part (a) and (c) it follows that  $z_3 > m - 1/\kappa(u_3)$  for  $\rho < 0.1$ . From part (b) and Lemma 6.11 it follows that  $z_3 > 0.25$  if  $\rho \ge 0.1$  for  $0 < u_3 \le 0.2$  which finishes the proof.  $\Box$ 

We proceed with the last part of the proof of the Stability complexity theorem in Region B, Proposition 6.3.

**Proof of Proposition 6.3:** We notice that for  $M_2 < \tilde{M}_2$  we get  $u_3 > u_{max}$  and  $0 < \kappa(u_3) < 1/2$ .

A necessary condition for Neimark-Sacker bifurcation was that

$$Q = q_{12}z_3^2m + q_{02}z_3^2 + q_{21}z_3m^2 + q_{11}z_3m + q_{01}z_3 + q_{20}m^2 + q_{10}m + q_{00} = 0,$$

where

$$\begin{aligned} q_{12} &= -\kappa(u_3)^2 \mathcal{K} < 0, \\ q_{02} &= -\kappa(u_3)^2 < 0, \\ q_{21} &= -\kappa(u_3)^2 < 0, \\ q_{11} &= \kappa(u_3)(1 - u_3\kappa(u_3) + \kappa(u_3) - \mathcal{K}(1 - \kappa(u_3)) < 2\kappa(u_3)^2, \\ q_{01} &= \kappa(u_3)(\kappa(u_3) - 2) < 0, \\ q_{20} &= \kappa(u_3)c, \\ q_{10} &= e^{-u_3} - \kappa(u_3)^2 < 0, \\ q_{00} &= -1 + \kappa(u_3) < 0, \end{aligned}$$

and  $c = \kappa(u_3) - e^{-u_3}$ .

We get  $Q/\kappa(u_3) < Am^2 + Bm + C$  where  $A = c - z_3\kappa(u_3)$ ,  $B = 2z_3\kappa(u_3)$  and  $C = (\kappa(u_3) - 2)z_3$ . The discriminant of the expression in *m* is  $D = 4AC - B^2 = (az_3 + b)z_3$ , where  $a = 8\kappa(u_3)(1 - \kappa(u_3)) > 0$  and  $b = 4c(\kappa(u_3) - 2)$ . Because  $z_3 > u_3$  (Lemma 6.5) we get

$$az_3 + b > au_3 + b = 4(2 - 4\kappa(u_3) + e^{-u_3}\kappa(u_3) + \kappa(u_3)^2) > 0.$$

Observing that C < 0 we can conclude that Q < 0 for  $u_3 > u_{max}$  and in this case there are no Neimark-Sacker bifurcations.  $\Box$ 

## 7. PROOFS OF LEMMAS

#### **Proof of Lemma 3.3:**

(a) Differentiating h we get

$$h' = \frac{w - 1 - \ln w}{(w - 1)^2},$$

which is positive for w > 1. Thus, (a) is proved.

- (b) Calculating h'' we get  $\xi(w)(w-1)^{-3}$ , where  $\xi(w) = -w+1/w+2\ln w$ . Since  $\xi'(w) = -(w-1)^2 w^{-2} < 0$ and  $\xi(1) = 0$  we get  $\xi(w) < 0$  for w > 1. Thus, h'' < 0 and (b) is proved.
- (c)  $\lim_{w\to\infty} h = \infty$  because  $w(w-1)^{-1} \to 1$  and  $\ln w \to \infty$  for  $w \to \infty$ . Series expansion of  $\ln w$  around w = 1 gives w(1 (w-1)/2) < h < w for w > 1 from which follows  $\lim_{w\to 1_+} h = 1$  and (c) is proved.
- (d) This property follows from (c) and (a).
- (e) *h* is increasing, so this property follows from (a) and the definition of  $\kappa$  (2).  $\Box$

Proof of Lemma 5.5: Calculations give

$$\mathcal{K}=\frac{1}{z}-\frac{1}{e^z-1}>0,$$

because  $e^{z_3} - 1 > z_3$ . The derivative of  $\mathcal{K}$  is

$$-\frac{1}{z^2} + \frac{e^z}{(e^z - 1)^2}.$$

The derivative is negative if  $z^2 < \frac{(e^z-1)^2}{e^z}$ . But

$$\frac{(e^z-1)^2}{e^z} = e^z + e^{-z} - 2 > 1 + z + \frac{z^2}{2} + \frac{z^3}{6} + 1 - z + \frac{z^2}{2} - \frac{z^3}{6} - 2 = z^2.$$

Further

$$\lim_{z \to 0} \mathcal{K} = \lim_{z \to 0} \frac{e^z - 1 - z}{z(e^z - 1)} = \lim_{z \to 0} \frac{\frac{z^2}{2} + \cdots}{z(z + \cdots)} = \frac{1}{2},$$

and

$$\mathcal{K}(u_{max}) = \frac{1}{u_{max}} - \frac{2 - u_{max}}{u_{max}} = 1 - \frac{1}{u_{max}}$$

because  $u_{max}e^{u_{max}} = 2e^{u_{max}} - 2$  (from (8)) implies  $e^{u_{max}} - 1 = \frac{u_{max}}{2-u_{max}}$ .  $\Box$ 

**Proof of Lemma 5.6:** Calculating  $z_3$  as a function of w on the bifurcation curve we get

$$z_3 = \ln\left(\frac{e^{-u_3}(w^2 - w) + w\ln w - 2w + 2}{1 + w\ln w - w}\right).$$

Calculating the derivative of  $e^{z_3}$  we get

$$\frac{l(w)}{(1+w\ln w - w)^2}$$

where

$$l(w) = e^{-u_3}(3w - 1 + w^2 \ln w - 2w^2) - 1 + w - \ln w.$$

Differentiating *l* we get  $l'(w) = l_1(w)/w$ , where

$$l_1(w) = (2w^2 \ln w - 3w^2 + 3w)e^{-u_3} + w - 1.$$

Differentiating  $l_1$  we get

$$l_1'(w) = l_2(w) = 1 + (3 + 4w \ln(w) - 4w)e^{-u_3},$$

and the derivative of  $l_2$  is  $4 \ln w e^{-u_3}$  which is positive for w > 1. Because  $l_2(1) = 1 - e^{-u_3} > 0$  and  $l_1(1) = l(1) = 0$ , we get l(w) > 0 for w > 1 and  $e^{z_3}$  and  $z_3$  is an increasing function in w. Observing that  $w \ln w - 2w + 2 = 0$  for  $w = w_{max}$  we obtain  $z_3(\rho_{max}) = u_{max} - u_3$ .  $\rho = 0$  is equivalent to  $w = e^{u_3}$  and calculations give  $z_3 = 0$  for  $w = e^{u_3}$ .  $\Box$ 

**Proof of Lemma 5.7:** Differentiating v with respect to  $\rho$  we get

$$\frac{\eta'(\rho+1) + \mathcal{A} - \eta}{(\rho+1)^2}.$$

To see that the derivative is positive we use the properties of  $\eta$  asserting that  $\eta$  is increasing in w and thus, also in  $\rho$  and  $\eta \leq \mathcal{A}$ . Direct substitutions give v(0) = 0 and  $v(\rho_{max}) = \mathcal{A}$ .  $\Box$ 

**Proof of Lemma 5.8:** From (b) in Lemma 3.3 follows that  $\frac{d\eta}{dw}$  is a decreasing function in *w*. The chain rule gives  $\frac{d\eta}{d\rho} = \frac{d\eta}{dw}e^{u_3}$  and we get  $\frac{d\eta}{d\rho} < s$ . Integration of the last inequality with respect to  $\rho$  gives the result.

**Proof of Lemma 5.9:** We start by proving the properties of *s*. Note first that

$$\frac{d\eta}{d\rho} = \frac{d\eta}{dw} \cdot \frac{dw}{d\rho} = \frac{dh}{dw} \frac{dw}{d\rho},$$

$$\frac{d\eta}{d\rho} = h'(v)v = \frac{v - 1 - \ln v}{(v - 1)^2}v,$$
(19)

and for  $\rho = 0$ ,

where  $v = e^{u_3}$ . This gives an explicit formula for *s*. The derivative of (19) with respect to *v* is

$$\frac{v\ln v - 2(v-1) + \ln v}{(v-1)^3} > 0,$$

for  $1 < v < w_{max}$  (the positivity of numerator is established by differentiating it twice). Thus, *s* is an increasing function of *v* and *u*<sub>3</sub>. Since  $\ln v = v - 1 - \frac{(v-1)^2}{2} + O((v-1)^3)$ , (19) gives  $\lim_{u_3 \to 0} s = \lim_{v \to 1} s = 1/2$ . For  $u_3 = u_{max}$  we have to estimate *s* for  $v = w_{max}$ . Then we get (remember that  $v \ln v = 2(v-1)$  for  $v = w_{max}$ ).

$$s = \frac{v - 1 - \frac{2(v-1)}{v}}{(v-1)^2}v = \frac{v-2}{v-1}$$

Because  $w_{max} < 5$  we get s < 3/4.

Now we prove the properties for  $\sigma$ . Calculations give

$$\frac{\partial \sigma}{\partial \rho} = \frac{\xi \rho^2 e^{u_3} + \xi^2 \rho + u_3 \rho^2 e^{u_3} - \ln(\rho + 1)(\xi \rho^2 e^{u_3} + 2\rho \xi e^{u_3} + \xi^2)}{(\rho e^{u_3} + \xi)^2 \rho^2 (1 - e^{-u_3})},$$

where  $\xi = e^{u_3} - 1$ . Using Lemma 5.10 we get

$$(\rho+2)\sigma_n < \rho^2(a\rho+b),$$

where  $\sigma_n$  is the numerator of  $\frac{\partial \sigma}{\partial \rho} a = e^{u_3}(u_3 + 1 - e^{u_3}) < 0$  and  $b = -e^{2u_3} + 2u_3e^{u_3} + 1$ . We notice that b = 0 for  $u_3 = 0$  and  $b' = 2e^{u_3}(-e^{u_3} + 1 + u_3) < 0$ . Thus, we conclude  $\frac{\partial \sigma}{\partial \rho} < 0$ .

Now it remains to consider

$$\frac{\partial \sigma}{\partial u_3} = \frac{\partial h}{\partial u_3} (\rho + 1) e^{u_3} - (1/\kappa(u_3))' = \frac{w - 1 - \ln w}{(w - 1)^2} w - \frac{e^{u_3} - 1 - u_3}{(e^{u_3} - 1)^2}$$

But the first term is known from the first part of this proof to increase in w and thus, also in  $u_3$ . Calculations give  $\frac{\partial \sigma}{\partial u_3} = 0$  for  $w = e^{u_3}$  and we conclude  $\frac{\partial \sigma}{\partial u_3} > 0$  for  $w > e^{u_3}$ .  $\Box$ 

**Proof of Lemma 5.10:** Both sides of the inequality are zero for t = 0 and the derivative of the left hand side is greater than the derivative of the right hand side for t > 0. The lemma follows directly from these facts.  $\Box$ 

**Proof of Lemma 5.11:** We split the proof of Lemma 5.11 into two major parts labeled (a) and (b) below. The second of these will, again, be split into three subparts.

(a) We first claim that: *P* is positive for  $0 < u_3 \le 1$  for any *v*.

We prove the statement above as follows: If *P* is considered as a second order polynomial in  $\nu$  the discriminant is  $-k^3(4\kappa(u_3)(1-u_3\kappa(u_3))+k)$ .  $\kappa_1(u_3) = 4\kappa(u_3)(1-u_3\kappa(u_3)) = 4\kappa(u_3)e^{-u_3}$  is a decreasing function in  $u_3$  and  $\kappa_1(1) > 0.93$ . Taking into account that  $-2/3 < -1/u_{max} < k < -1/2$  we conclude that the discriminant is positive and because the coefficient for  $\nu^2$  is positive we get P > 0 for all  $\nu$ .

(b) The second claim is that: P is positive for  $1 < u_3 < u_{max}$  and  $0 < v \le \mathcal{A} = 2 - 1/\kappa(u_3)$ .

We are going to prove the above statement by splitting it into three parts. In proving these parts we use estimates of k given in Lemma 5.5 above.

(i) The first part reads: For  $v \in [0, 2 - 1/\kappa(u_3)]$  the minimum

$$P^* = (4\kappa(u_3) - 2)k^2 + (u_3\kappa(u_3) + 4\kappa(u_3) - 2)k + \kappa(u_3),$$

of *P* is taken for  $v = 2 - 1/\kappa(u_3)$ . The above statement follows by first observing that the coefficient for *v* in *P* is negative because  $\kappa(u_3) > 1/2$  and -1 < k < 0. The minimum of *P* is taken at

$$\nu_* = -\frac{2k\kappa(u_3) + k^2}{2\kappa(u_3)k^2} = -\left(\frac{1}{k} + \frac{1}{2\kappa(u_3)}\right) > 0$$

Because k > -2/3 we get  $2 + \frac{1}{k} < \frac{1}{2} < \frac{1}{2\kappa(u_3)}$  from which follows  $v_* > 2 - 1/\kappa(u_3)$  and *P* decreases in the interval  $[0, 2 - 1/\kappa(u_3)]$ . After calculating  $P(2 - 1/\kappa(u_3)) = P^*$  the statement follows.

(ii) The next statement we are going to prove reads: If  $1 \le u_3 < u_{max}$  the minimum  $P_-$  of  $P^*$  for  $k \in [-1/2, -1/u_{max}]$  is taken for  $k = -1/u_{max}$ . Observe that both coefficients for  $k^2$  and k are positive in  $P^*$  so minimum is taken for some negative

$$k_{-} = -\frac{u_{3}\kappa(u_{3}) + 4\kappa(u_{3}) - 2}{2(4\kappa(u_{3}) - 2)} = -\frac{1}{2} - \frac{u_{3}\kappa(u_{3})}{2(4\kappa(u_{3}) - 2)}.$$

Because  $\frac{\kappa(u_3)}{4\kappa(u_3)-2} > \frac{1}{2}$  for  $1/2 < \kappa(u_3) < 1$  we get

$$\frac{u_3\kappa(u_3)}{2(4\kappa(u_3)-2)} > \frac{1}{4}$$

for  $u_3 \ge 1$  and  $k_- < -3/4 < -1/u_{max}$ . Now, (ii) holds.

(iii) The last statement reads:  $P^* > 0$  for  $k = -1/u_{max}$  and  $1 < u_3 < u_{max}$ . When proving (iii), we first note that  $P_-$  is decreasing in  $u_3$  for  $1 < u_3 < u_{max}$  because

$$P^* = (\kappa(u_3)(2k+1)^2 + ku_3\kappa(u_3) - 2(k+k^2),$$

and  $\kappa(u_3)$  is decreasing and  $u_3\kappa(u_3) = 1 - e^{-u_3}$  is increasing. Calculating  $P^*$  for  $u_3 = u_{max}$  and  $k = -1/u_{max}$  we get zero because  $\kappa(u_{max}) = 1/2$ . Now, (iii) follows.  $\Box$ 

Proof of Lemma 6.4:

$$\kappa(t)^{2}e^{t} = \frac{e^{t} + e^{-t} - 2}{t^{2}} > \frac{1 + t + \frac{t^{2}}{2} + \frac{t^{3}}{6} + 1 - t + \frac{t^{2}}{2} - \frac{t^{3}}{6} - 2}{t^{2}} = 1. \square$$

**Proof of Lemma 6.5:** From Lemma 6.4 follows that Condition 3.6 is satisfied for  $z_3 = u_3$ . Because  $\kappa(z_3)$  is decreasing for increasing  $z_3$ , Condition 3.6 is satisfied also for  $z_3 < u_3$ .  $\Box$ 

**Proof of Lemma 6.6:**  $0 < q_- < 1$  is equivalent to  $0 < \kappa(u_3)q_- < \kappa(u_3)$  and  $0 < e^{-u_3} = 1 - u_3\kappa(u_3) < \kappa(u_3)$  which clearly holds. The derivative of  $1/\kappa(u_3)$  with respect to  $u_3$  is  $(\kappa(u_3) - e^{-u_3})u_3^{-1}\kappa(u_3)^{-2}$  which is less than one, because  $(\kappa(u_3) - e^{-u_3})u_3^{-1}\kappa(u_3)^{-2} < 1$  is equivalent to  $\kappa(u_3) - e^{-u_3} < (u_3\kappa(u_3))\kappa(u_3) = (1 - e^{-u_3})\kappa(u_3)$  which holds because  $\kappa(u_3) < 1$ . Thus, the derivative of  $q_-$  is less than zero.  $\Box$ 

**Proof of Lemma 6.7:** We start with observing that  $-\mathcal{K}'z_3 < \mathcal{K}$  for all positive  $z_3$ . Indeed, the inequality is after calculations seen to be equivalent to  $\mathcal{K}_z = e^{z_3}z_3/(e^{z_3} - 1) > 1$ . But the derivative of  $\mathcal{K}_z$  is  $e^{z_3}(e^{z_3} - z_3 - 1)(e^{z_3} - 1)^{-2} > 0$  and  $\lim_{z_3 \to 0^+} \mathcal{K}_z = 1$  so the inequality is always true. The derivative of Q with respect to  $z_3$  is  $Q' = 2Q_{z2}z_3 + Q'_{z2}z_3^2 + Q_{z1} + Q'_{z1}z_3$  where  $Q_{z2} = -\kappa(u_3)^2(m\mathcal{K} + 1)$  and  $Q_{z1} = q_{21}m^2 + q_{11}m + q_{01}$ .

Because m > 0 and  $\mathcal{K} > 0$  according to Lemma 5.5 we easily get

$$2Q_{z2}z_3 + Q'_{z2}z_3^2 = -\kappa(u_3)^2(2(m\mathcal{K}+1)z_3 + \mathcal{K}'mz_3^2) < 0,$$

using  $\mathcal{K}'z_3 + \mathcal{K} > 0$ .

We observe that  $q_{11} = \tilde{q}_{11} - \kappa(u_3)(1 - \kappa(u_3))\mathcal{K}$  and we get

$$Q_{z1} + Q'_{z1}z_3 = \tilde{Q}_{z1} - \kappa(u_3)(1 - \kappa(u_3))m(\mathcal{K} + \mathcal{K}'z_3),$$

where  $\tilde{Q}_{z1} = q_{21}m^2 + \tilde{q}_{11}m + q_{01}$  and  $\tilde{q}_{11} = \kappa(u_3)(1 - u_3\kappa(u_3) + \kappa(u_3))$ .

Because  $q_{01}, q_{21} < 0$ ,  $\tilde{Q}_{z1}$  can be considered as a second order polynomial in *m* which is always negative if  $Q_{q1} = 4q_{01}q_{21} - \tilde{q}_{11}^2 > 0$ . We observe that from  $\tilde{q}_{11}/\kappa(u_3) < 2\kappa(u_3)$  (see estimates in third part of the proof of Proposition 6.9) follows

$$\frac{Q_{q1}}{\kappa(u_3)^2} > 4(-\kappa(u_3))(\kappa(u_3) - 2) - 4\kappa(u_3)^2 = 8\kappa(u_3)(1 - \kappa(u_3)) > 0.$$

So  $\tilde{Q}_{z1}$  is negative and thus, also  $Q_{z1} + Q'_{z1}z_3$  is negative.  $\Box$ 

**Proof of Lemma 6.11:**  $z_3$  is the solution to the equation

$$e^{z_3} = \kappa(u_3)\kappa(z_3)e^{u_3}M_1(M_0e^{-u_3}-1).$$

From  $\kappa(u_3)\kappa(z_3) < e^{-u_3}$  we get  $e^{z_3} < M_1(M_0e^{-u_3} - 1)$  and from Lemma 6.4 follows

$$\frac{e^{z_3}}{e^{-z_3/2}} > \frac{e^{z_3}}{\kappa(z_3)} = \kappa(u_3)e^{u_3}M_1(M_0e^{-u_3}-1),$$

implying  $z_3 > \frac{2}{3} \ln(\kappa(u_3)e^{u_3}M_1(M_0e^{-u_3}-1)).$ 

The expression for  $\ln(M_1(M_0e^{-u_3}-1))$  is the same as in the case Condition 3.6 is satisfied. There, in the proof of Lemma 5.6, it was proved that  $\ln(M_1(M_0e^{-u_3}-1))$  is increasing with *w*. Also  $e^{z_3}/\kappa(z_3)$  is increasing in  $z_3$ . Indeed, the derivative of  $e^{z_3}/\kappa(z_3)$  is

$$\frac{e^{2z_3}((1+z_3)e^{z_3}-1-2z_3)}{(e^{z_3}-1)^2} > \frac{e^{2z_3}z_3^2}{(e^{z_3}-1)^2} > 0.$$

Thus,  $z_3$  must increase with w.  $\Box$ 

**Proof of Lemma 4.2:** If Condition 3.6 holds, then the conclusion of the lemma follows from arguments given in [2] (page 407-408). We proceed by assuming that  $P_3$  belongs to region B. The necessary criterion for one eigenvalue to be equal to one is  $k_{fold} = 1 + \alpha + \beta + \gamma = 0$ , where  $\alpha$ ,  $\beta$ ,  $\gamma$  are the coefficients in the characteristic polynomial of the Jacobian in case B (16)-(18). Calculations give

$$k_{fold} = \frac{z_3(M_0 - e^{u_3})(\mathcal{K} + 1)}{M_0} > 0,$$

and we conclude that there are no such bifurcations in this case.

The necessary criterion for one eigenvalue equal to -1 is  $k_{flip} = 1 - \alpha + \beta - \gamma = 0$ . Calculations give

$$k_{flip} = \frac{1}{M_0\kappa(u_3)} [(z_3\kappa(u_3)(1-\mathcal{K}) + 2(e^{-u} + \kappa(u_3)))M_0 + e^{u_3}z_3\kappa(u_3)(1-\mathcal{K}) + 2e^{u_3}(1+\kappa(u_3))] > 0.$$

Thus, there are no such bifurcations in this case, too.  $\Box$ 

## 8. SUMMARY

In this paper we proved that parameter values for which an unsaturated invading carnivore may stabilize a discrete oscillatory plant-herbivore system cannot exist. We have assumed unsaturated herbivores and carnivores that both specialize on their prey. Many continuous systems like those based on the Rosenzweig model<sup>[5]</sup> do not display the same property. This was, for instance, pointed out by Freedman and Waltman<sup>[3]</sup> and Oksanen, Fretwell, Arruda, and Niemelä<sup>[18]</sup>. Actually, unsaturated invading specializing carnivores have a stabilizing impact on continuous ecosystems whereas we have excluded their possibilities for displaying such properties in discrete ecosystems completely. This implies discrete or seasonal food-chains to be less stable than the corresponding continuous or non-seasonal food-chains. Such stability properties have classically been related to food-chain length<sup>[1, 19, 20, 24]</sup>, so this gives possibilities for expecting differences in the length of various food-chains as long as the components remain specialized.

It will be of vital importance for future studies to clarify what dynamical consequences invading generalist predators might have in both types of ecosystems. It is likely that they have a stabilizing impact on both types of ecosystems<sup>[21]</sup>. However, this is not clear for all parameter values. It is also far from clear what specialists remain in the ecosystem after invasion of generalists and whether generalist stabilized ecosystems contain space for longer specialist chains than non-stabilized ones. Another important question for future study is of course whether adjustable reproductive behavior<sup>[22]</sup> or adaptive dynamics<sup>[23]</sup> might alter the stability patterns and promote longer food-chains.

An important issue that have been left out of this study is the question of under what conditions local stability implies global stability of the fixed points in the positive plant-herbivore quadrant and in the positive octant. It is in general difficult to construct useful Lyapunov functions for discrete systems, see e.g., [25]. Thus, oscillatory dynamics may exist in our system also when, for instance  $P_3$  (equilibrium coexistence of all species) is locally stable. In fact, such dynamics have been noted numerically ([2], p406, remark (b)), but the phenomenon was very unstable.

A partial answer to the above question could be obtained if the type of Neimark-Sacker bifurcation is determined. As the system is dissipative a supercritical Neimark-Sacker bifurcation is expected, but this does not exclude subcritical bifurcations. In our case, Kuznetsov's criterion has a lot of terms<sup>[9]</sup>. The functions B and C has 19 and 46 non-zero terms, respectively, and the needed eigenvectors take complicated forms. Analytical proofs are therefore, hardly possible. All our numerical calculations based on that criterion done so far confirm this bifurcation to be supercritical. In fact, the NS3-curve ends at a fold-Neimark-Sacker bifurcation where

$$M_0 = \frac{e^{u_3}\kappa(u_3)}{2\kappa(u_3) - 1}, \ M_1 = \frac{2\kappa(u_3) - 1}{1 - \kappa(u_3)}, \ u_3 = \frac{1}{M_2}$$

and the  $F_3$  and NS2-curves intersect.

If subcritical bifurcations could be excluded analytically, then more is known about conditions for existence of oscillatory solutions. This is a partial answer to the global stability problem. If subcritical Neimark-Sacker bifurcations would turn out to be possible in system (1), then both stable and oscillatory behavior must coexist, since the solutions of (1) remain positive and bounded. A proof of existence of subcritical Neimark-Sacker bifurcations in (1) would therefore be an indication of interesting dynamical behavior.

## ACKNOWLEDGMENTS

We thank the anonymous referee for useful suggestions.

## REFERENCES

- [1] May, R. M. (1971). Stability in multispecies community models. *Mathematical Biosciences*, *12*, 59-79.
- [2] Lindström, T. (2002). On the dynamics of discrete food-chains: Low- and high-frequency behavior and chaos. *Journal of Mathematical Biology*, *45*, 396-418.
- [3] Freedman, H. I., & Waltman, P. (1977). Mathematical analysis of some three-species food-chain models. *Mathematical Biosciences*, *33*, 257-276.
- [4] Pelletier, J. D. (2000). Are large complex ecosystems more unstable? A theoretical reassessment with predator switching. *Mathematical Biosciences*, *163*, 91-96.
- [5] Rosenzweig, M. L. (1973). Exploitation in three throphic levels. *The American Naturalist*, 107(954), 275-294.
- [6] Elton, C. A. (1958). The ecology of invasions by animals and plants. London: Methuen.
- [7] Petrushev, P. P., & Popov, V. A. (1987). *Rational approximation of real functions*. Cambridge: Cambridge Press.
- [8] Guckenheimer, J., & Holmes, P. (1983). Nonlinear oscillations, dynamical systems, and bifurcations of vector Fields. Berlin: Springer-Verlag.
- [9] Kuznetsov, Yu. A. (1998). Elements of applied bifurcation theory. New York: Springer.
- [10] Bainov, D. D., & Simeonov, P. S. (ed.) (1989). *Systems with impulsive effect, theory and applications*. Chichester: Ellis Harwood.
- [11] Bainov, D. D., & Simeonov, P. S. (1993). Impulsive differential equations: Periodic solutions and applications. Volumn 66 of Pitman Monographs and Surveys in Pure and Applied Mathematics.
- [12] Lakshmikantham, W., Bainov, D. D., & Simeonov, P. S. (1989). Theory of impulsive differential equations, Volumn 6 of World Scientific Ceries in Modern Mathematics. Singapore: World Scientific.
- [13] Borror, D. J., De Long, D. M., & Triplehorn, C. A. (1976). *An introduction to the study of insects (4th edition)*. New York: Holt, Rinehart, and Winston.
- [14] Butler, G., & Waltman, P. (1986). Persistence in dynamical systems. *Journal of Differential Equations*, 63, 255-263.
- [15] Schur, J. (1917). Über Potenzreihen, die im Innern des Einheitskreises beschränkt sind. Journal für die reine und angewandte Mathematik, 147, 205-232.
- [16] Schur, J. (1918). Über Potenzreihen, die im Innern des Einheitskreises beschränkt sind. Journal für

die reine und angewandte Mathematik, 148, 122-145.

- [17] Cohn, A. (1922). Über die Anzahl der Wurzeln einer algebraischen Gleichung in einem Kreise. *Matematische Zeitschrift, 14*, 110-148.
- [18] Oksanen, L., Fretwell, S. D., Arruda, J., & Niemelä, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, 118(2), 240-261.
- [19] Pimm, S. L., & Lawton, J. H. (1977). Number of trophic levels in ecological communities. *Nature*, 268, 329-331.
- [20] Pimm, S. L. (1982). Food webs. New York: Chapman and Hall.
- [21] Hanski, I., Hansson, L., & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, *60*, 353-367.
- [22] Gyllenberg, M., Hanski, I., & Lindström, T. (1996). A predator-prey model with optimal suppression of reproduction in the prey. *Mathematical Biosciences*, 134, 119-152.
- [23] Lacitgoula, D., & Tebaldi, C. (2005). Effects of ecological differentiation on Lotka-Volterra systems for species with behavioral adaption and variable growth rates. *Mathematical Biosciences*, 194, 95-123.
- [24] May, R. M. (1974). Ecosystem patterns in randomly fluctuating environments, in: Progress in Theoretical Biology (edited by Rosen, R., & Snell, F.). New York: Academic Press.
- [25] Goh, B. S. (1980). *Management and analysis of biological populations*. Amsterdam and New York: Elsevier Scientific Publishing Company.