



Ordinary Differential Equations/Dynamical Systems

## Convergence to equilibrium in competitive Lotka–Volterra and chemostat systems

### *Convergence vers l'équilibre pour des systèmes compétitifs de Lotka–Volterra et du Chémostat*

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#### ABSTRACT

We study a generalized system of ODE's modeling a finite number of biological populations in a competitive interaction. We adapt the techniques in Jabin and Raoul [8] and Champagnat and Jabin (2010) [2] to prove the convergence to a unique stable equilibrium.

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#### RÉSUMÉ

Nous étudions un système généralisé d'équations différentielles modélisant un nombre fini de populations biologiques en interaction compétitive. En adaptant les techniques de Jabin et Raoul [8] et de Champagnat et Jabin (2010) [2], nous prouvons la convergence vers un unique équilibre stable.

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#### Version française abrégée

Nous étudions le comportement en temps grand de modèles de dynamique de populations. On considère un nombre fini de sous-populations, correspondant chacune à un trait ou type différent. Ces populations interagissent entre elles de façon compétitive. En notant  $n_i(t)$  l'effectif de la sous-population numéro  $i$ , un des modèles les plus classiques est le système de Lotka–Volterra compétitif

$$\frac{d}{dt}n_i = \left( r_i - \sum_j b_{ij}n_j \right) n_i, \quad i = 1, \dots, N,$$

où  $b_{ij} \geq 0$ . On se place ici dans le cadre plus général du système

$$\frac{d}{dt}n_i(t) = \left[ r_i - \int_{\Omega} K_i(\alpha) L\left(\alpha, \sum_j B_j(\alpha)n_j(t)\right) dP(\alpha) \right] n_i(t), \quad i = 1, \dots, N,$$

avec  $(\Omega, P)$  un espace mesurable. Ce système peut s'interpréter comme un modèle avec ressources généralisées.

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En utilisant les techniques développées dans [8] pour une version continue du premier modèle, et dans [2], on peut facilement montrer

**Théorème.** *Supposons que  $\forall \alpha \in \Omega$ ,  $L(\alpha, \cdot)$  est une fonction  $C^1$  sur  $\mathbb{R}$ , positive sur  $\mathbb{R}_+$ , de dérivée  $L'(\alpha, \cdot)$  uniformément bornée en  $\alpha$  sur tout compact de  $\mathbb{R}$ , que  $L(\cdot, 0)$  est bornée, que  $K$  et  $B$  sont des fonctions positives bornées appartenant à  $L^1(dP(\alpha))$  et que*

- (i) (Compétition stricte) *Pour tout  $\alpha \in \Omega$ ,  $L(\alpha, \cdot)$  est strictement croissante et pour tout  $1 \leq i \leq n$ ,  $r_i < \int_{\Omega} K_i(\alpha)L(\alpha, \infty) dP(\alpha)$  où  $L(\alpha, \infty) := \lim_{x \rightarrow +\infty} L(\alpha, x) \in (0, +\infty]$ .*
- (ii) (Symétrie) *Il existe  $C_i > 0$  tq  $B_i(\alpha) = C_i K_i(\alpha)$ .*
- (iii) (Non extinction) *Pour tout  $i$ ,  $r_i > \int_{\Omega} K_i(d\alpha)L(\alpha, 0) dP(\alpha)$ .*
- (iv) (Non dégénérescence) *Pour  $I \subset \{1, \dots, N\}$ , soit  $\mathbb{R}^I$  l'ensemble des  $n \in \mathbb{R}^N$  tels que  $n_i = 0$  pour tout  $i \notin I$ . Pour tout  $I \subset \{1, \dots, N\}$  il y a au plus un  $n \in \mathbb{R}^I$  tq*

$$r_i - \int_{\Omega} K_i(\alpha)L\left(\alpha, \sum_{j=1}^N B_j(\alpha)n_j\right) dP(\alpha) = 0, \quad \forall i \in I.$$

Alors  $\exists! \bar{n} = (\bar{n}_1, \dots, \bar{n}_N) \in \mathbb{R}_+^N \setminus \{0\}$ , tel que pour toute solution  $n(t) = (n_1, \dots, n_N)$  du modèle généralisé avec une donnée initiale  $n_i(0) > 0 \forall i$ , on a que  $n(t) \rightarrow \bar{n}$ , quand  $t \rightarrow +\infty$ .

En particulier ce résultat implique

**Proposition.** *Supposons que  $r_i > 0$  pour tout  $i$  et que la matrice  $b_{ij}$  vérifie*

$$\exists C \in (\mathbb{R}_+^*)^N \text{ tq } C_i b_{ij} = b_{ji} C_j, \quad \text{et} \quad \sum_{ij} u_i u_j b_{ij} C_i > 0, \quad \forall u \in \mathbb{R}^N \setminus \{0\}.$$

Alors  $\exists! \bar{n} = (\bar{n}_1, \dots, \bar{n}_N) \in \mathbb{R}_+^N \setminus \{0\}$  tel que pour toute solution  $n(t) = (n_1, \dots, n_N)$  du premier modèle avec donnée initiale  $n_i(0) > 0 \forall i$ ,  $n(t) \rightarrow \bar{n}$ , quand  $t \rightarrow +\infty$ .

Nous obtenons également un résultat de convergence pour un système classique en chémotaxie couplant dynamiques de populations et de ressources.

### 1. Introduction

We study the long time behavior of models of population dynamics. We consider a finite number of subpopulations whose dynamics is governed by a system of competitive ODEs (in the sense of Hirsch, see e.g. [6]). We denote by  $n_i(t)$ ,  $i = 1, \dots, N$ , the number of individuals of the subpopulation  $i$ .

The most classical models are competitive Lotka–Volterra equations

$$\frac{d}{dt} n_i = \left( r_i - \sum_j b_{ij} n_j \right) n_i, \quad i = 1, \dots, N, \tag{1}$$

where  $b_{ij} \geq 0$ , and the models with a finite number of resources

$$\frac{d}{dt} n_i = \left( -d_i + \sum_{k=1}^K I_k \eta_{ki} \right) n_i, \quad I_k = \frac{I_k^0}{1 + \sum_{i=1}^N \mu_{ki} n_i}, \tag{2}$$

where  $\eta_{ki} \geq 0$  and the  $I_k$  are given by the Holling II functional response.

This type of system appears in biology when one studies the dynamics of a system of interacting species (see [7,5,9]). It also appears in Trait Substitution Sequence models, where one considers a population structured by a continuous phenotype (see Eq. (3)), where only a small number of traits are present (see [10,1]). These models have been used to develop the theory of Adaptative Dynamics (see [10,1,3]).

Previous asymptotic studies on this type of equations concern either very general properties (the existence of a carrying simplex [6]), or precise results but only for low dimensional systems ( $N \leq 3$  [13]), under strong assumptions of the coefficients (for instance, the matrix  $(b_{ij})$  is supposed to be diagonal dominant, see [7]), or only on local properties (the equilibrium population is locally stable, or populations  $n_i$  do not vanish).

Both Eqs. (1) and (2) may be interpreted as discrete versions of continuous models. To each  $i$ , corresponds a phenotypic trait  $x_i \in \mathbb{R}^d$ , and then posing  $n(t, x) = \sum_{i=1}^N n_i(t) \delta_{x_i}$ , one finds that Eq. (1) is equivalent to

$$\partial_t n(t, x) = \left( r(x) - \int_{\mathbb{R}^d} b(x, y)n(t, dy) \right) n(t, x), \tag{3}$$

with  $r_i = r(x_i)$  and  $b_{ij} = b(x_i, x_j)$ .

The long time behavior of the continuous model (3) was studied in [8], with a proof of convergence to the unique stable equilibrium for a symmetric  $b$  defining a positive operator. The case with resources is essentially contained in [2], which generalizes the derivation of [4]. The derivation of such evolution models has recently been the subject of intense studies; an important step is often the study of the asymptotic in time of systems like (3), see for example [11], especially Chapter 2.

In the continuous case, the large time asymptotic is for instance connected to the issue of speciation, or how from a continuum of traits a few well separated ones (the “species”) are selected; in the discrete case, one is rather concerned about survival or extinction of each subpopulations. From a rigorous mathematical point of view, a result in the continuous case does not imply anything for the discrete one. However it is easy to apply the techniques developed in [8] and [2] to the discrete models; that is our aim.

First of all, we consider the very general equation

$$\frac{d}{dt} n_i(t) = \left[ r_i - \int_{\Omega} K_i(\alpha) L \left( \alpha, \sum_j B_j(\alpha) n_j(t) \right) dP(\alpha) \right] n_i(t), \quad i = 1, \dots, N, \tag{4}$$

with  $(\Omega, P)$  any measurable space. We prove the following:

**Theorem 1.** Assume that  $\forall \alpha \in \Omega$ ,  $L(\alpha, \cdot)$  is  $C^1$  on  $\mathbb{R}$  and non-negative on  $\mathbb{R}_+$ , with derivative  $L'(\alpha, \cdot)$  bounded on compact subsets of  $\mathbb{R}$ , uniformly in  $\alpha \in \Omega$ , that  $L(\alpha, 0)$  is bounded, that  $K$  and  $B$  are bounded, non-negative, in  $L^1(dP(\alpha))$  and that

(i) (Strict competition) For all  $\alpha \in \Omega$ ,  $L(\alpha, \cdot)$  is strictly increasing and

$$r_i < \int_{\Omega} K_i(\alpha) L(\alpha, \infty) dP(\alpha), \quad \text{for all } 1 \leq i \leq N,$$

where  $L(\alpha, \infty) := \lim_{x \rightarrow +\infty} L(\alpha, x) \in (0, +\infty]$ .

(ii) (Symmetry) There exists  $C_i > 0$  s.t.  $B_i(\alpha) = C_i K_i(\alpha)$ .

(iii) (Non-extinction) For any  $i$ ,  $r_i > \int_{\Omega} K_i(\alpha) L(\alpha, 0) dP(\alpha)$ .

(iv) (Non-degeneracy) For any  $I \subset \{1, \dots, N\}$ , let  $\mathbb{R}^I$  be the set of  $n \in \mathbb{R}^N$  s.t.  $n_i = 0$  for all  $i \notin I$ . For all  $I \subset \{1, \dots, N\}$ , there exists at most one  $n \in \mathbb{R}^I$  s.t.

$$r_i - \int_{\Omega} K_i(\alpha) L \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j \right) dP(\alpha) = 0, \quad \forall i \in I. \tag{5}$$

Then there exists a unique  $\bar{n} = (\bar{n}_1, \dots, \bar{n}_N) \in \mathbb{R}_+^N$  with  $\bar{n} \neq 0$ , s.t. for any solution  $n(t) = (n_1, \dots, n_N)$  to (4) with initial data  $n_i(0) > 0$  for any  $i$ ,  $n(t) \rightarrow \bar{n}$ , as  $t \rightarrow +\infty$ .

Eq. (4) is a generalization, with a possibly infinite number of resources, of the model (2), containing the Lotka–Volterra system (1). In this case,

**Proposition 1.** Assume that  $r_i > 0$  for all  $i$  and that the matrix  $b_{ij}$  satisfies

$$\exists C \in (\mathbb{R}_+^*)^N \text{ s.t. } C_i b_{ij} = b_{ji} C_j, \quad \text{and} \quad \sum_{ij} u_i u_j b_{ij} C_i > 0, \quad \forall u \in \mathbb{R}^N \setminus \{0\}, \tag{6}$$

then there exists a unique  $\bar{n} = (\bar{n}_1, \dots, \bar{n}_N) \in \mathbb{R}_+^N$  with  $\bar{n} \neq 0$ , s.t. for any solution  $n(t) = (n_1, \dots, n_N)$  to (1) with initial data  $n_i(0) > 0$  for any  $i$ ,  $n(t) \rightarrow \bar{n}$ , as  $t \rightarrow +\infty$ .

Thus, in Lotka–Volterra systems which are symmetric in the sense of (6), the competition between a mutant trait and a resident population leads to a unique stationary state, regardless of the initial population state. This is precisely the assumption needed in [1] to apply a limit of large population and rare mutations to an individual-based model. In particular, Theorem 2.7 of [1] applies to symmetric competitive Lotka–Volterra systems.

Finally the same techniques and Lyapunov functionals also apply to some systems where the resources themselves solve a differential equation, in particular the so-called “chemostat” consisting of

$$\frac{d}{dt} n_i = \left( -d_i + \sum_{k=1}^K f_k(I_k) \eta_{ki} \right) n_i, \tag{7}$$

coupled with

$$\frac{d}{dt} I_k = I_k^0 - I_k - f_k(I_k) \sum_{i=1}^N \mu_{ki} n_i, \quad I_k(0) \geq 0. \tag{8}$$

If  $f_k = \text{Id}$  and one assumes that the resources adapt themselves faster than the individuals, taking  $dI_k/dt = 0$  in (8), one recovers (2).

The coupled system (7)–(8) was introduced and studied in [12] together with other of the same types but only with one resource:  $K = 1$ . However adapting the proof of Theorem 1, one can show the following:

**Theorem 2.** Assume that the  $I_k^0$  are positive, and that

- (i) (Strict competition)  $f_k$  is  $C^1$  with  $f'_k > 0$  on  $\mathbb{R}_+$ ,  $f_k(0) = 0$  and  $\eta_{ki} > 0$  for all  $1 \leq i \leq N$ ,  $1 \leq k \leq K$ .
- (ii) (Symmetry) There exists  $C_i > 0$  s.t.  $\mu_{ki} = C_i \eta_{ki}$ .
- (iii) (Non-explosion, non-extinction)  $\forall i, \sum_k \eta_{ki} f_k(0) < d_i < \sum_{k=1}^K \eta_{ki} f_k(I_k^0)$ .
- (iv) (Non-degeneracy) For any  $I \subset \{1, \dots, N\}$ , let  $\mathbb{R}^I$  be the set of  $n \in \mathbb{R}^N$  s.t.  $n_i = 0$  for all  $i \notin I$ . For all  $I \subset \{1, \dots, N\}$ , there exists at most one  $n \in \mathbb{R}^I$  s.t.

$$d_i - \sum_{k=1}^K f_k \left( \psi_k \left( \sum_{i=1}^N \mu_{ki} n_i \right) \right) \eta_{ki} = 0, \quad \forall i \in I,$$

where  $\psi_k(n)$  is the inverse function of  $(I_k^0 - x)/f_k(x)$  on  $[0, I_k^0]$ .

Then there exists a unique  $(\bar{n}, \bar{I}) = (\bar{n}_1, \dots, \bar{n}_N, \bar{I}_1, \dots, \bar{I}_K) \in \mathbb{R}_+^{N+K}$  with  $\bar{n} \neq 0$ , s.t. for any solution  $(n(t), I(t))$  to (7) and (8) with initial data  $n_i(0) > 0$  for any  $i$ ,  $(n(t), I(t)) \rightarrow (\bar{n}, \bar{I})$ , as  $t \rightarrow +\infty$ .

**2. Proof of Proposition 1**

Define the matrix  $m_{ij} = C_i b_{ij}$ . Note that  $m$  is symmetric and positive definite. Hence there exists an orthonormal basis of eigenvectors  $U^i$ ,  $i = 1, \dots, N$ , and corresponding eigenvalues  $\lambda_i > 0$ .

Then put  $L(\alpha, \cdot) = \text{Id}$ ,  $\Omega = \{1, \dots, N\}$ ,  $P = \frac{1}{N} \sum_{i=1}^N \delta_i$ ,  $B_j(\alpha) = \sqrt{\lambda_\alpha} U_j^\alpha$ ,  $K_i(\alpha) = C_i^{-1} \sqrt{\lambda_\alpha} U_i^\alpha$  and note that

$$\begin{aligned} \sum_{j=1}^N b_{ij} n_j &= \frac{1}{C_i} \sum_{j=1}^N m_{ij} n_j = \frac{1}{C_i} \left[ M \left( \sum_{\alpha} U^\alpha(U^\alpha, n) \right) \right]_i = \frac{1}{C_i} \sum_{\alpha=1}^N \lambda_\alpha U_i^\alpha \left( \sum_{j=1}^N U_j^\alpha n_j \right) \\ &= \int_{\Omega} K_i(\alpha) L \left( \sum_{j=1}^N B_j(\alpha) n_j \right) dP(\alpha). \end{aligned}$$

Therefore Eq. (4) indeed yields (1) in that particular case.

Conditions (i) and (ii) of Theorem 1 are obviously satisfied. Condition (iii) holds since  $r_i > 0$  for all  $i$  and  $L(\alpha, 0) = 0$ . As for condition (iv), assume that for a subset  $I$  one has two vectors  $n_j^\gamma$ ,  $\gamma = 1, 2$ , s.t.  $n_i^\gamma = 0$  for  $i \notin I$  and

$$r_i = \int_{\Omega} K_i(\alpha) L \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j^\gamma \right) dP(\alpha) = \sum_{j=1}^N b_{ij} n_j^\gamma, \quad \forall i \in I.$$

Put  $\delta n = n^1 - n^2$  and simply note that  $\delta n_i \sum_{j=1}^N b_{ij} \delta n_j = 0$ ,  $i = 1, \dots, N$ .

This means that  $\delta n = 0$  and proves (iv) since  $\sum_{i,j=1}^N C_i b_{ij} \delta n_i \delta n_j = 0$ . Hence the proposition is implied by Theorem 1.

**3. Proof of Theorem 1**

The proof is based on the study of the Lyapunov functional

$$F(n) = \int_{\Omega} H \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j \right) dP(\alpha) - \sum_{i=1}^N C_i r_i n_i,$$

for  $H(\alpha, \cdot)$  the antiderivative of  $L(\alpha, \cdot)$  with  $H(\alpha, 0) = 0$  and hence strictly convex.

### 3.1. $F$ is a convex Lyapunov functional

Let  $n$  be a solution to (4). Then by a direct computation

$$\frac{d}{dt} F(n(t)) = - \sum_{i=1}^N C_i n_i \left[ \int_{\Omega} K_i(\alpha) L \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j \right) dP(\alpha) - r_i \right]^2.$$

Therefore  $F(n(t))$  is non-increasing and its derivative in time vanishes only on stationary solutions to (4), i.e.  $F$  is a strict Lyapunov functional.

Thanks to condition (i),  $\frac{\partial F}{\partial n_i} \geq C_i \int_{\Omega} K_i(\alpha) L(\alpha, \frac{K_i(\alpha)}{C_i} n_i) dP(\alpha) - r_i \geq a > 0$ , if  $n_i$  is large enough. Therefore,  $\nabla F(n) \cdot n \geq a' \|n\|$  for  $\|n\|$  large enough and  $F(n) \rightarrow +\infty$  when  $\|n\| \rightarrow +\infty$ . Hence  $n(t)$  is uniformly bounded.

Let  $n \in \mathbb{R}_+^N$  be a steady-state of (4) and let  $I$  be the set of  $i$  s.t.  $n_i > 0$ . Then, for any  $i \in I$  one needs to have  $\int_{\Omega} K_i(\alpha) L(\alpha, \sum_{j=1}^N B_j(\alpha) n_j) dP(\alpha) = r_i$ . By condition (iv) there is at most one such solution for every  $I$ , and with only a finite number of possible  $I$ ,  $F$  has then a finite number of steady-states.

Classical Lyapunov functionals' techniques then entail that the solution  $n(t)$  to (4) converges to a steady-state  $\tilde{n}$  for any initial condition  $n(0)$ .

$F$  is convex and any local minimum on  $\mathbb{R}_+^N$  is global. Indeed as  $L$  is increasing,  $\sum_{i,k} \frac{\partial^2 F}{\partial n_i \partial n_k} \xi_i \xi_k \geq 0$ , since

$$\frac{\partial^2 F}{\partial n_i \partial n_k} = \int_{\Omega} B_i(\alpha) B_k(\alpha) L' \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j \right) dP(\alpha).$$

Since (4) has a finite number of stationary solutions, this clearly implies that  $F$  admits a unique global minimizer  $\bar{n}$ . Otherwise,  $F$  would reach its minimum on the whole segment linking two distinct minimizers.

### 3.2. Uniqueness of the ESS

Any local minimizer  $n \in \mathbb{R}_+^N$  of the functional  $F$  necessarily satisfies  $\forall i$

$$\int_{\Omega} K_i(\alpha) L \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j \right) dP(\alpha) \geq r_i, \quad \text{with equality if } n_i > 0. \tag{9}$$

This is the usual definition of an Evolutionarily Stable Strategy in adaptive dynamics (see [3]). There is at most one ESS,  $\bar{n}$  and being an ESS is hence a necessary and sufficient condition to be the global minimizer of  $F$ .

Take two  $n^\gamma \in \mathbb{R}_+^N$ ,  $\gamma = 1, 2$ , satisfying (9) and compute (with the convention  $2 + 1 = 1$ )

$$0 \geq \sum_{\gamma=1,2} \sum_i C_i n_i^\gamma \left( r_i - \int_{\Omega} K_i(\alpha) L \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j^{\gamma+1} \right) dP(\alpha) \right).$$

This last quantity is equal to (thanks to (9))

$$\sum_{\gamma=1,2} \sum_i C_i (n_i^\gamma - n_i^{\gamma+1}) \left( r_i - \int_{\Omega} K_i(\alpha) L \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j^{\gamma+1} \right) dP(\alpha) \right)$$

and to

$$\int_{\Omega} \left( \sum_j B_j(\alpha) n_j^1 - \sum_j B_j(\alpha) n_j^2 \right) \left( L \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j^1 \right) - L \left( \alpha, \sum_{j=1}^N B_j(\alpha) n_j^2 \right) \right) dP(\alpha).$$

As  $L(\alpha, \cdot)$  is strictly increasing, this implies that for  $P$  a.e.  $\alpha$ ,  $\sum_{i=1}^N B_i(\alpha) (n_i^1 - n_i^2) = 0$  and by (iv), it means that  $n^1 = n^2$ .

### 3.3. Conclusion of the proof of Theorem 1

Assume that  $n_i(0) > 0$  for all  $1 \leq i \leq N$ . We know from Section 3.1 that  $n(t)$  converges to a steady-state  $\tilde{n}$  when  $t \rightarrow \infty$ . If  $\tilde{n}$  does not satisfy (9), there exists  $i \in \{1, \dots, N\}$  such that  $\lambda_i := r_i - \int_{\Omega} K_i(\alpha) L(\alpha, \sum_{j=1}^N B_j(\alpha) \tilde{n}_j) dP(\alpha) > 0$ .

Since  $n_i(0) > 0$ ,  $n_i > 0$  at all times, and the linearized equation around  $\tilde{n}$  shows that  $n$  cannot converge to  $\tilde{n}$ . Indeed  $\frac{d}{dt} (n - \tilde{n})_i = (\lambda_i + O(\|n - \tilde{n}\|))(n - \tilde{n})_i \geq \frac{\lambda_i}{2} (n - \tilde{n})_i$ , provided that  $\|n - \tilde{n}\|$  is small enough.

Therefore,  $\tilde{n} = \bar{n}$ , and the proof of Theorem 1 is completed.

#### 4. Proof of Theorem 2

First note that the equilibria  $(\bar{n}, \bar{I})$  of (7)–(8) are exactly those of coupled with  $\bar{I}_k = \psi_k(\sum_i \mu_{ki} \bar{n}_i)$ . Taking  $\Omega = \{1, \dots, K\}$ ,  $L(\alpha, x) = f_\alpha(I_\alpha^0) - f_\alpha(\psi_\alpha(x))$  and  $P(d\alpha) = \sum_{k=1}^K \delta_k(d\alpha)$ . This has exactly the form of (4). Therefore the definition of the ESS, its existence and uniqueness are exactly the same as in the proof of Theorem 1.

Denote  $(\bar{n}, \bar{I})$  the unique ESS of the system. The equivalent of  $F$  is

$$\tilde{F}(n, I) = \sum_{i=1}^N C_i(n_i - \bar{n}_i \log n_i) + \sum_{k=1}^K (I_k - f_k(\bar{I}_k) g_k(I_k)), \quad (10)$$

with  $g_k$  an antiderivative of  $1/f_k$  on  $(0, +\infty)$ . Note that  $\tilde{F}$  is well-defined if  $n_i > 0$  for  $i$  such that  $\bar{n}_i > 0$ . Consider a solution of (7)–(8) with such an initial condition. We compute as previously

$$\frac{d\tilde{F}}{dt} \leq - \sum_k \frac{(f_k(I_k) - f_k(\bar{I}_k))^2}{f_k(I_k)} \sum_i \mu_{ik} \bar{n}_i - \sum_k \frac{f_k(I_k) - f_k(\bar{I}_k)}{f_k(I_k)} (I_k - \bar{I}_k),$$

which is a Lyapunov functional as the  $f_k$  are increasing. Note that the right-hand side vanishes iff  $I_k = \bar{I}_k$  for all  $k$ , making the functional degenerate.

As we are in a finite dimensional setting, we correct this by considering  $G = \tilde{F} + \gamma \sum_k (I_k - \bar{I}_k) \sum_i \mu_{ki} (n_i - \bar{n}_i)$ . Taking  $\gamma$  small enough

$$\frac{dG}{dt} \leq -\frac{1}{2} \sum_k \frac{(f_k(I_k) - f_k(\bar{I}_k))^2}{f_k(I_k)} \sum_i \mu_{ki} \bar{n}_i - \sum_k \frac{f_k(I_k) - f_k(\bar{I}_k)}{f_k(I_k)} (I_k - \bar{I}_k) - \frac{\gamma}{2} \sum_k f_k(I_k) \left( \sum_i \mu_{ki} (n_i - \bar{n}_i) \right)^2.$$

By assumption (iv), this vanishes only if  $(n, I) = (\bar{n}, \bar{I})$ . Theorem 2 now simply follows from Lyapunov's Theorem.

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