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Convergence to equilibrium in competitive Lotka-Volterra and chemostat systems

Nicolas Champagnat¹, Pierre-Emmanuel Jabin^{1,2}, Gaël Raoul³

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 [8] and [2] to prove the convergence to a unique stable equilibrium.

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

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

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

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

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 α 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

$$n(t) \longrightarrow \bar{n}, \text{ quand } t \rightarrow +\infty.$$

En particulier ce résultat implique

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

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

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 $n_i(0) > 0 \forall i$,

$$n(t) \longrightarrow \bar{n}, \text{ quand } t \rightarrow +\infty.$$

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

1 Introduction

We study the long time behaviour 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

$$\frac{d}{dt}n_i = \left(r_i - \sum_j b_{ij} n_j \right) n_i, \quad i = 1 \dots N, \quad (1.1)$$

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

$$\frac{d}{dt}n_i = \left(-d_i + \sum_{k=1}^K I_k \eta_{ki} \right) n_i, \quad (1.2)$$

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

$$I_k = \frac{I_k^0}{1 + \sum_{i=1}^N \mu_{ki} n_i}. \quad (1.3)$$

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 equation (1.5), (1.7) on this matter), 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).

Note that both equations (1.1) and (1.2) may be interpreted as discrete versions of continuous models. To each subpopulation corresponds a phenotypic trait $x_i \in \mathbb{R}^d$, and then posing

$$n(t, x) = \sum_{i=1}^N n_i(t) \delta_{x_i}, \quad (1.4)$$

one finds that Eq. (1.1) for instance is equivalent to

$$\partial_t n(t, x) = \left(r(x) - \int_{\mathbb{R}^d} b(x, y) n(t, dy) \right) n(t, x), \quad (1.5)$$

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

The long time behaviour of the continuous model (1.5) (with bounded initial data instead of Dirac masses) was studied in [8]. For a symmetric b defining a positive operator, the convergence to the unique stable equilibrium was proved. For the case with resources, the result 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; while those are more complex than the relatively simple result presented here, an important step is often the study of the asymptotic in time of systems like (1.5). We refer for example to [11] and especially Chapter 2.

The study of the discrete or continuous models corresponds to slightly different biological questions; in the continuous case, it 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

$$\frac{d}{dt} n_i(t) = \left[r_i - \int_{\Omega} K_i(\alpha) L \left(\alpha, \sum_j B_j(\alpha) n_j(t) \right) dP(\alpha) \right] n_i(t), \quad i = 1 \dots N, \quad (1.6)$$

with (Ω, P) any measurable space, or in the continuous case

$$\partial_t n(t, x) = \left[r(x) - \int_{\Omega} K(x, \alpha) L \left(\alpha, \int_{\mathbb{R}^d} B(y, \alpha) n(t, dy) \right) dP(\alpha) \right] n(t, x). \quad (1.7)$$

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 $r_i < \int_{\Omega} K_i(\alpha) L(\alpha, \infty) dP(\alpha)$ 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.

$$r_i - \int_{\Omega} K_i(\alpha) L\left(\alpha, \sum_{j=1}^N B_j(\alpha) n_j\right) dP(\alpha) = 0, \quad \forall i \in I. \quad (1.8)$$

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 (1.6) with initial data $n_i(0) > 0$ for any i ,

$$n(t) \longrightarrow \bar{n}, \text{ as } t \rightarrow +\infty.$$

Note that, if one had $r_i > \int K_i(\alpha) L(\alpha, \infty) dP(\alpha)$ for some i , then $n_i(t) \rightarrow +\infty$ if $n_i(0) > 0$. Assumption (i) hence ensures the non-explosion of the system.

Eq. (1.6) could be directly derived from simple biological considerations. It assumes that the reproduction rate of a population of type i (or with trait x_i) is the difference between a fixed rate depending only on the trait and a competitive interaction with the other populations, resulting from the interaction with the environment. The state of each component of this environment (indicated by different values of α) is given by the sum

$$\sum_j B_j(\alpha) n_j(t).$$

Each such component has some independent effect on the reproduction. To get the total reproduction rate one sums over those.

Eq. (1.6) is hence an obvious generalization, with a possibly infinite number of resources, of the model (1.2). It also contains the Lotka-Volterra system (1.1). In this case, Theorem 1 gives

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

$$\exists C \in (\mathbb{R}_+^*)^N \text{ s.t. } C_i b_{ij} = b_{ji} C_j, \text{ and } \sum_{ij} u_i u_j b_{ij} C_i > 0 \quad \forall u \in \mathbb{R}^N \setminus \{0\}, \quad (1.9)$$

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 (1.1) with initial data $n_i(0) > 0$ for any i ,

$$n(t) \longrightarrow \bar{n}, \text{ as } t \rightarrow +\infty.$$

This result shows that, in Lotka-Volterra systems which are symmetric in the sense of (1.9), 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, Thm. 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 ressources themselves solves a differential equation. This is in particular the case of the so-called “chemostat” which consists of the system composed of

$$\frac{d}{dt}n_i = \left(-d_i + \sum_{k=1}^K f_k(I_k)\eta_{ki} \right) n_i, \quad (1.10)$$

coupled with

$$\frac{d}{dt}I_k = I_k^0 - I_k - f_k(I_k) \sum_{i=1}^N \mu_{ki}n_i, \quad I_k(0) \geq 0. \quad (1.11)$$

Note that if $f_k = Id$ and if one assumes that the ressources adapt themselves faster than the individuals and hence take $dI_k/dt = 0$ in (1.11), one recovers (1.2)–(1.3).

The coupled system (1.10)–(1.11) was introduced and studied in [12] together with other of the same types but only with one ressource: $K = 1$. However adapting the proof of Th. 1, one can show for any number of ressources

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 (1.10) and (1.11) with initial data $n_i(0) > 0$ for any i ,

$$(n(t), I(t)) \longrightarrow (\bar{n}, \bar{I}), \text{ as } t \rightarrow +\infty.$$

2 Proof of Prop. 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

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

Therefore Eq. (1.6) indeed yields (1.1) in that particular case.

Conditions (i) and (ii) of Theorem 1 are obviously satisfied. Conditions (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^γ , $\gamma = 1, 2$, 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 $\delta n_i \sum_{j=1}^N b_{ij} \delta n_j = 0$ pour $i = 1 \dots N$.

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. $\square$

Note that the same argument works in the continuous case and Eq. (1.5) is a particular case of (1.7) for $x \in O$ a bounded domain. The condition on b is

$$C(x) b(x, y) = C(y) b(y, x), \quad \int_{O^2} C(x) b(x, y) n(x) n(y) dx dy > 0 \quad \forall n \neq 0.$$

One still puts $L(\xi) = \xi$. Notice that $C(x) b(x, y)$ defines a compact, selfadjoint and positive operator on $L^2(O)$. Diagonalizing the operator, one gets

$$C(x) b(x, y) = \sum_{\alpha} \lambda_{\alpha} f_{\alpha}(x) f_{\alpha}(y),$$

with $\lambda_{\alpha} > 0$ the eigenvalues, tending to $+\infty$ and f_{α} the corresponding normalized eigenvector. It is hence enough to take $\Omega = \mathbb{N}$ and $K(x, \alpha) = \sqrt{\lambda_{\alpha}} f_{\alpha}(x)$.

In the particular case where $b(x, y) = b(x - y)$ on the whole $\mathbb{R}^d$ and $C = 1$, by Fourier transform, the condition on b means that $\hat{b} > 0$. One then takes $\Omega = \mathbb{R}^d$ and

$$K(x, \alpha) = (\cos(\alpha \cdot x) \sqrt{\hat{b}(\alpha)}, \sin(\alpha \cdot x) \sqrt{\hat{b}(\alpha)}).$$

3 Proof of Theorem 1

The proof is based on the study of the following Lyapunov functional

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

where for all $\alpha \in \Omega$, $H(\alpha, \cdot)$ is the antiderivative of $L(\alpha, \cdot)$ such that $H(\alpha, 0) = 0$ and hence strictly convex.

3.1 F is a strict Lyapunov functional

Let n be a solution to (1.6). 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 (1.6), i.e. F is a strict Lyapunov functional for the system (1.6).

Thanks to condition (i),

$$\frac{\partial F}{\partial n_i} \geq C_i \left(\int_{\Omega} K_i(\alpha) L\left(\alpha, \frac{K_i(\alpha)}{C_i} n_i\right) dP(\alpha) - r_i \right) \geq a > 0$$

if n_i is large enough. Therefore, there is a constant $a' > 0$ s.t. $\nabla F(n) \cdot n \geq a' \|n\|$ if $\|n\|$ is large enough. This implies that $F(n) \rightarrow +\infty$ when $\|n\| \rightarrow +\infty$, and entails that $n(t)$ is uniformly bounded.

Let $n \in \mathbb{R}_+^N$ be a steady-state of (1.6) and let I be the set of i s.t. $n_i > 0$. Then, for any $i \in I$ one needs to have

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

By condition (iv) there is at most one such solution for every I , and there are 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 (1.6) converges to a steady-state $\tilde{n}$ for any initial condition $n(0)$.

3.2 The functional F is convex

Compute

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

Hence as L is increasing

$$\sum_{i,k} \frac{\partial^2 F}{\partial n_i \partial n_k} \xi_i \xi_k = \int_{\Omega} \left(\sum_i \xi_i B_i(\alpha) \right)^2 L'\left(\alpha, \sum_{j=1}^N B_j(\alpha) n_j\right) dP(\alpha) \geq 0.$$

F is therefore convex and any local minimum on $\mathbb{R}_+^N$ is global.

Since (1.6) 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.

The object of the next subsection is to prove that $\bar{n}$ satisfies a stronger property: this is the unique ESS of the system.

3.3 Uniqueness of the ESS

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

$$\begin{aligned} \int_{\Omega} K_i(\alpha) L\left(\alpha, \sum_{j=1}^N B_j(\alpha) n_j\right) dP(\alpha) &= r_i, \quad \forall i \text{ s.t. } n_i > 0, \\ \int_{\Omega} K_i(\alpha) L\left(\alpha, \sum_{j=1}^N B_j(\alpha) n_j\right) dP(\alpha) &\geq r_i, \quad \forall i \text{ s.t. } n_i = 0. \end{aligned} \quad (3.1)$$

This condition corresponds to the usual definition of an Evolutionarily Stable Strategy in adaptive dynamics (see for instance [3]). It turns out that there exists at most one ESS, $\bar{n}$. Hence being an ESS is a necessary and sufficient condition to be the global minimizer of F .

Indeed take two $n^\gamma \in \mathbb{R}_+^N$, $\gamma = 1, 2$ satisfying (3.1) and compute

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

This last quantity is equal to (thanks to (3.1))

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

and to

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

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

3.4 Conclusion of the proof of Thm. 1

Assume that $n_i(0) > 0$ for all $1 \leq i \leq N$. We know from Subsection 3.1 that $n(t)$ converges to a steady-state $\tilde{n}$ when $t \rightarrow \infty$.

If $\tilde{n}$ does not satisfy (3.1), there exists $i \in \{1, \dots, N\}$ such that

$$\lambda_i := r_i - \int_{\Omega} K_i(\alpha) L \left(\alpha, \sum_{j=1}^N B_j(\alpha) \tilde{n}_j \right) dP(\alpha) > 0.$$

Since $n_i(0) > 0$, $n_i > 0$ at all times, and the linearized equation around $\tilde{n}$ shows that n cannot converge to $\tilde{n}$:

$$\begin{aligned} \frac{d}{dt}(n - \tilde{n})_i &= (\lambda_i + O(\|n - \tilde{n}\|)) (n - \tilde{n})_i \\ &\geq \frac{\lambda_i}{2} (n - \tilde{n})_i, \end{aligned}$$

provided that $\|n - \tilde{n}\|$ is small enough.

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

4 Proof of Theorem 2

First note that the equilibria $(\bar{n}, \bar{I})$ of (1.10)–(1.11) are exactly those of

$$\frac{d}{dt}n_i = \left[-d_i + \sum_{k=1}^K \eta_{ki} f_k \left(\psi_k \left(\sum_{i=1}^N \mu_{ki} n_i \right) \right) \right] n_i, \quad (4.1)$$

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 $P(d\alpha) = \sum_{k=1}^K \delta_k(d\alpha)$, (4.1) has exactly the form of (1.6). Therefore the definition of the ESS, its existence and uniqueness are exactly the same as in the proof of Theorem 1.

Let us denote $(\bar{n}, \bar{I})$ the unique ESS of the system. The exact equivalent of the functional F would be

$$\tilde{F}(n, I) = \sum_{i=1}^N C_i (n_i - \bar{n}_i \log n_i) + \sum_{k=1}^K (I_k - f_k(\bar{I}_k) g_k(I_k)), \quad (4.2)$$

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 $\bar{n}_i > 0$. Let us consider a solution of (1.10)–(1.11)

with such an initial condition. Then $n_i(t) > 0$ for all $t \geq 0$ and i such that $\bar{n}_i > 0$, and we compute

$$\begin{aligned} \frac{d}{dt} \tilde{F}(n(t), I(t)) &= \sum_i (n_i - \bar{n}_i) \left(\sum_k C_i \eta_{ki} f_k(I_k) - C_i d_i \right) \\ &\quad + \sum_k \frac{f_k(I_k) - f_k(\bar{I}_k)}{f_k(I_k)} \left(I_k^0 - I_k - f_k(I_k) \sum_i \mu_{ki} n_i \right) \end{aligned}$$

Recalling that $(\bar{n}, \bar{I})$ is a stationary solution, one gets

$$\begin{aligned} \frac{d\tilde{F}}{dt} &= \sum_i \sum_k (n_i - \bar{n}_i) \mu_{ki} (f_k(I_k) - f_k(\bar{I}_k)) + \sum_i (n_i - \bar{n}_i) \left(\sum_k \mu_{ki} f_k(\bar{I}_k) - C_i d_i \right) \\ &\quad - \sum_k \sum_i \mu_{ki} (n_i - \bar{n}_i) (f_k(I_k) - f_k(\bar{I}_k)) \\ &\quad + \sum_k \frac{f_k(I_k) - f_k(\bar{I}_k)}{f_k(I_k)} \left(I_k^0 - I_k - f_k(I_k) \sum_i \mu_{ki} \bar{n}_i \right) \end{aligned}$$

As $(\bar{n}, \bar{I})$ is an ESS then

$$(n_i - \bar{n}_i) \left(\sum_k \mu_{ki} f_k(\bar{I}_k) - C_i d_i \right) = n_i \left(\sum_k \mu_{ki} f_k(\bar{I}_k) - C_i d_i \right) \leq 0.$$

Finally, recalling that $\sum_i \mu_{ki} \bar{n}_i = (I_k^0 - \bar{I}_k)/f_k(\bar{I}_k)$

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

which is indeed 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 . In that sense this Lyapunov functional is degenerate as now the I_k are not anymore connected to the n_i by an explicit relation.

As we are in a finite dimension setting, it is easy to correct this problem. Consider instead of $\tilde{F}$

$$G = \tilde{F} + \gamma \sum_k (I_k - \bar{I}_k) \sum_i \mu_{ki} (n_i - \bar{n}_i).$$

Note that, since

$$\frac{d}{dt} \left(\sum_i C_i n_i + \sum_k I_k \right) \leq a - b \left(\sum_i C_i n_i + \sum_k I_k \right)$$

for explicit constants $a, b > 0$, all solutions to (1.10)–(1.11) enter in finite time the set $D = \{\sum_i C_i n_i + \sum_k I_k \leq a/b, I_k \geq c, \forall k \leq K\}$, where $c > 0$ is such that $c + f(c)b/a = \min_k I_k^0$.

Taking γ small enough and using the fact that f'_k is uniformly bounded from below, one simply gets that, on the set D ,

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

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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