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# Persistence in ecological models of competition for a single resource

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## Abstract

We show how the consideration of an intra-specific dependency in the population growth functions can explain a stable persistence of several species in competition for a single resource. This result is applied to a model of single-nutrient competition in the chemostat. *To cite this article: C. Lobry et al., C. R. Acad. Sci. Paris, Ser. I 340 (2005).*

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## Résumé

**Persistance dans les modèles écologiques de compétition pour une seule ressource.** Nous montrons comment la considération d'un terme de compétition intra-spécifique dans les lois de croissance permet d'expliquer la persistance stable de plusieurs espèces en compétition pour une même ressource. Ce résultat est appliqué à un modèle de compétition pour un seul substrat dans le chemostat. *Pour citer cet article: C. Lobry et al., C. R. Acad. Sci. Paris, Ser. I 340 (2005).*

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## Version française abrégée

Nous considérons le système différentiel dans  $\mathbb{R}^n$   $\dot{x}_i = x_i f_i(x_i, u)$  ( $i = 1, \dots, n$ ), soumis à la boucle de rétroaction  $u = -g(t, x)$ , et nous montrons sous des hypothèses assez générales qui sont satisfaites lorsque

- pour tout  $i$ , la fonction  $(x_i, u) \rightarrow f_i(x_i, u)$  est monotone décroissante par rapport à  $x_i$ , monotone croissante par rapport à  $u$ ,
- la fonction  $g(t, \cdot)$  converge uniformément vers une fonction  $x \mapsto r(x)$  strictement monotone par rapport à  $x$ ,
- la fonction  $f : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$  s'annule en un unique  $x^*$  dont toutes les composantes sont strictement positives,

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que  $x^*$  est globalement asymptotiquement stable.

En dynamique des populations, ce système s'interprète comme la compétition de  $n$  espèces  $x_i$  pour une même ressource  $u$ . La décroissance de  $f_i$  par rapport à  $x_i$  exprime une sorte de « compétition » à l'intérieur de chaque espèce pour l'accès au substrat, et le résultat exprime que si cette dernière est assez forte il y a coexistence de toutes les espèces en un sens fort.

La stabilité locale de l'équilibre est une trivialité qui se constate en vérifiant que la matrice jacobienne possède toutes ses valeurs propres strictement négatives. Le résultat de stabilité globale qui fait l'objet de cette note ne semble pas se trouver dans la littérature. La démonstration est élémentaire mais un peu technique. Elle exploite à fond le fait que les applications  $t \rightarrow (x_i(t), -g(t, x(t)))$  sont des applications à valeur dans  $\mathbb{R}^2$  et les hypothèses de monotonie.

L'idée de découpler certains problèmes de dynamique des populations « densité dépendant » (c'est-à-dire dans lequel les taux de croissances dépendent de la taille de la population) en un système « entrée-sortie » (où l'entrée représente la (ou les) ressource(s) et une rétroaction de la population sur la ressource n'est pas neuve. On peut citer, entre autres [16,15,1,2,4,5].

Dans [1,2], on décrit une très intéressante méthode générale de type « petit gain » (au sens de l'automatique), permettant de démontrer des résultats de stabilité globale pour des systèmes de type dynamique des populations. Cette méthode permettrait de démontrer notre résultat, mais sous une hypothèse beaucoup plus forte que les notes. En revanche la méthode exposée en [1,2] ne suppose pas que les  $x_i$  sont mono-dimensionnels.

Nous appliquons notre résultat à la démonstration de la coexistence de plusieurs espèces dans un modèle de croissance de micro-organismes en chémostat. Ce modèle est proche de celui proposé dans [4] en ce sens qu'il explique la coexistence par l'effet de l'augmentation de la densité ('crowding effect'), mais il en diffère en ce qu'il respecte la « conservation de la masse », ce qui est plus proche de la tradition des modèles de croissance en chémostat.

Une approche de ces questions par des fonctions de Liapunov non lisses est en cours de rédaction [6]. Une justification sur la base de considérations abiotiques (purements physiques) de notre modèle de croissance dans le chémostat est en cours de rédaction [14].

## 1. Introduction

We consider dynamical systems in  $\mathbb{R}^n$  with a scalar input  $u$ , of the following form

$$\dot{x}_i = \phi_i(x_i, u) = x_i f_i(x_i, u) \quad (i = 1, \dots, n). \quad (1)$$

We prove that under suitable assumptions detailed below the closed loop system  $\dot{x}_i = x_i f_i(x_i, u(t, x))$ , for a particular family of control laws  $u(\cdot, c)$ , possesses an equilibrium which is globally asymptotically stable. The result is stated in Section 2, proved in Section 3 and applied in Section 4 to a model of competition in the chemostat.

Our result is not a consequence of the general method proposed in [1,2] since it does not rely on the fact that a certain application is a contraction (see below). However, we assume that the  $x_i$ 's are one dimensional which is not a requirement of the method described in [1,2]. Finally, observe that the use of control-theoretic methods in populations dynamics is not new (see for instance [4,15]).

## 2. Statement of the main results

H1. The functions  $f_i$  are continuously differentiable in all their arguments.

H2. For each  $i \in \{1, \dots, n\}$ , there exists a strictly increasing function  $\psi_i : \mathbb{R}_+ \rightarrow \mathbb{R}$  such that

$$f_i(x_i, \psi_i(x_i)) = 0, \quad x_i \in \mathbb{R}_+.$$

Moreover,  $f_i(x_i, u) > 0$  if  $u > \psi_i(x_i)$  and  $f_i(x_i, u) < 0$  if  $u < \psi_i(x_i)$ .

We denote by  $\varphi_i : \mathbb{R} \rightarrow \mathbb{R}_+$  the inverse of the function  $\psi_i$ , extended by 0 for values smaller than  $\psi_i(0)$ .

In theoretical ecology, systems (1) can describe the behavior of a collection of  $n$  different species in the presence of a common resource  $u$ . Hypothesis H2 says that for each species the size of its population has a unique non-trivial stable equilibrium, provided the resource  $u$  is large enough.

We consider now the closed loop system

$$\dot{x}_i = \phi_i(x_i, -g(t, x)) \quad (i = 1, \dots, n) \tag{2}$$

along with the following hypothesis on the feedback  $u(t, x) = -g(t, x)$ .

H3. The function  $g$  is continuously differentiable, and the mappings  $\{g(t, \cdot)\}_{t \geq 0}$  converge in the  $\mathcal{C}^1$  norm, when  $t$  goes to  $+\infty$ , to a mapping  $r(\cdot)$  such that

$$\frac{\partial r}{\partial x_i}(x) \geq a_i > 0 \quad (i = 1, \dots, n) \quad \forall x.$$

Hypothesis H3 expresses that there is competition: the larger the size the population is, the smaller the available resource for growth is. The un-stationarity of the feedback is typically useful in applications when the resource depends dynamically on the overall size of the population.

Denote by  $\mathcal{P}$  the positive quadrant  $(\mathbb{R}_+^*)^n$ . The aim of the note is to give sufficient conditions for the solutions of (2) in  $\mathcal{P}$  to converge to a unique equilibrium point in  $\mathcal{P}$ .

H4. There exists  $x^* \in \mathcal{P}$  such that

$$f_i(x_i^*, -r(x^*)) = 0 \quad (i = 1, \dots, n).$$

**Remark 1.** From Hypotheses H2 and H3, it is straightforward to check that  $x^*$  is the unique equilibrium of the system (2) in  $\mathcal{P}$ , and that, for any other non-negative equilibrium  $\bar{x}$ , the inequality

$$r(\bar{x}) \leq r(x^*)$$

is satisfied.

**Proposition 2.1.** *Under Hypotheses H1–H4, any bounded solution of (2) with initial condition  $x(0) \in \mathcal{P}$  converges to  $x^*$ .*

**Remark 2.** In [1,2], a theory is developed for the purpose of proving stability of equilibria for systems of the form

$$\dot{X}_i = F_i(X_i, u), \quad X_i \in \mathbb{R}^{n_i}, \quad u \in \mathbb{R} \quad (i = 1, \dots, n)$$

when each sub-system is monotone. Since a one dimensional system is always monotone, one may wonder whether this theory applies to our model. As a matter of fact, it does but only in the particular case when the mapping  $u \rightarrow -r(\varphi_1(u), \dots, \varphi_n(u))$  is a contraction, which is a much stronger property than those satisfied by the systems we study. On the other hand, our result is restricted to  $n_i = 1$  for each  $i = 1, \dots, n$ .

**Proposition 2.2.** *Under Hypotheses H1–H3 and H4, the equilibrium point  $x^*$  is globally asymptotically stable on  $\mathcal{P}$ .*

### 3. Proof of Proposition 2.1: multi-phase plane analysis

The curves  $\phi_i(x_i, u) = 0$  can be viewed as the  $x_i$  nulcline (with reference to the classical phase analysis in the plane) that one can superpose on a same graph (see Fig. 1). We shall call it ‘multi-phase plane analysis’.

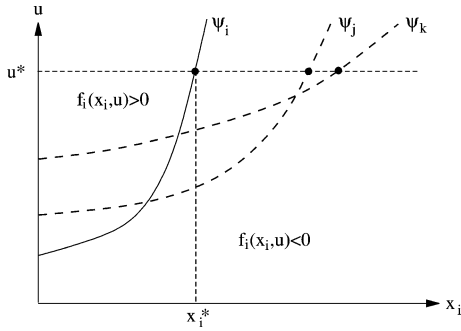


Fig. 1. Multi-phase plane analysis.

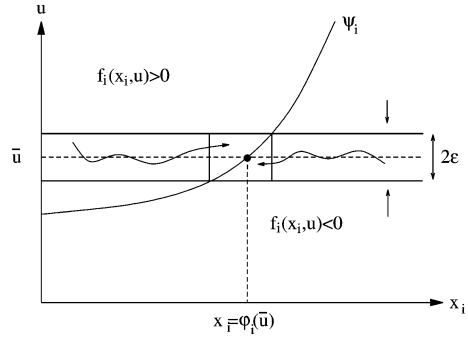


Fig. 2. Convergence into a box.

**Proof of Proposition 2.1.** Consider a bounded solution  $x(\cdot)$  of (2). Then the function  $u(t) = -g(t, x(t))$  is also bounded. When  $x(0) \in \mathcal{P}$ , it is clear that  $x(t) \in \mathcal{P}$  for any  $t \geq 0$ , due to the particular structure of the dynamics (1).  $\square$

If  $u(\cdot)$  converges to some  $\bar{u}$ , then for each  $i$ , the pair  $(x_i(t), u(t))$  enters the box  $[\varphi_i(\bar{u} - \epsilon), \varphi_i(\bar{u} + \epsilon)] \times [\bar{u} - \epsilon, \bar{u} + \epsilon]$  for any  $\epsilon > 0$  (by consideration of the signs of the functions  $f_i$ , see Fig. 2). Let  $\epsilon$  tends towards 0. We obtain that  $x(\cdot)$  converges towards  $\bar{x}$  such that  $\bar{x}_i = \varphi_i(\bar{u})$ , for each  $i = 1, \dots, n$ . From H4, we deduce that necessarily  $\bar{x} = x^*$ .

Assume now that  $u(\cdot)$  does not converge. Let  $u^-, u^+$  be  $\liminf_{t \geq 0} u(t)$ ,  $\limsup_{t \geq 0} u(t)$ , respectively. Denote  $x^- = \liminf_{t \geq 0} x(t)$ . One can prove that the following inequalities

$$x_i^- \geq \varphi_i(u^-) \quad (i = 1, \dots, n) \tag{3}$$

are then satisfied by proceeding by contradiction. Assume that (3) does not hold. Then take a sequence  $l_n \rightarrow +\infty$  such that  $x(l_n)$  converges towards  $x^-$ . There exist  $\epsilon > 0$  and an index  $i$  such that  $x_i(l_n) < \varphi_i(u^-) - \epsilon$  and  $\varphi_i(u(l_n)) > \varphi_i(u^-) - \epsilon$  for large enough  $n$ . Then one has  $x_i(l_n) < \varphi_i(u(l_n))$ , which implies that  $\dot{x}_i(l_n) = \varphi_i(x_i(l_n), u(l_n)) > 0$ . This yields a contradiction with the convergence of  $x_i(l_n)$  towards  $x_i^-$ .

Consider now a sequence  $t_n \rightarrow +\infty$  such that  $\dot{u}(t_n) \leq 0$  and  $u(t_n) \rightarrow u^-$ . One can also require on the sequence  $x(t_n)$  to converge to some  $\bar{x}$ . From (3), we deduce that  $\bar{x}$  satisfies the inequalities  $\bar{x}_i \geq \varphi_i(u^-)$  for any  $i$ . Indeed,  $\bar{x}$  necessarily fulfills the equalities

$$\bar{x}_i = \varphi_i(u^-) \quad (i = 1, \dots, n). \tag{4}$$

If  $\bar{x}_i$  was strictly larger than  $\varphi_i(u^-)$  for some  $i$ , one could write

$$\dot{u}(t_n) = -\frac{\partial g}{\partial t}(t_n, x(t_n)) - \sum_{i=1}^n \frac{\partial g}{\partial x_i}(t_n, x(t_n)) x_i(t_n) f_i(x_i(t_n), u(t_n))$$

and claim that  $f_i(x_i(t_n), u(t_n)) < 0$  for  $n$  large enough. Then the properties of  $g(\cdot)$  given in H3 would ensure the existence of a number  $N$  such that  $\dot{u}(t_N) > 0$ , which is a contradiction.

Finally, Eqs. (4) imply that  $\bar{x}$  is an equilibrium of the system (2) and  $u^- = -r(\bar{x})$ . According to Remark 1, the following inequality is then fulfilled.

$$u^- = -r(\bar{x}) \geq -r(x^*) = u^*.$$

In a similar way, one can prove the inequality  $u^+ \leq u^*$  and conclude that  $u(\cdot)$  converges to  $u^*$

**Proof of Proposition 2.2.** Since Proposition 2.1 ensures that  $x^*$  is globally attractive, it suffices to prove that it is locally stable. This can be done by computing the Jacobian matrix of (2) at  $x^*$ , and checking that all its eigenvalues have strictly negative real parts.  $\square$

#### 4. Single-nutrient competition in the chemostat

The classical model of a mixed culture in competition for a single substrate in a chemostat is given by the following equations (see [18,17,7]).

$$\begin{aligned} \dot{s} &= - \sum_{j=1}^n \frac{\mu_j(s)}{k_j} x_j + D(s_{in} - s), \\ \dot{x}_i &= x_i(\mu_i(s) - D) \quad (i = 1, \dots, n). \end{aligned} \tag{5}$$

The variables  $s$  and  $x_i$  are, respectively, the substrate and the  $i$ -th micro-organism concentrations,  $D$  is the dilution rate of the input flow of feed concentration  $s_{in}$ . The activity of the  $i$ -th micro-organism on the substrate is characterized by the growth function  $\mu_i(\cdot)$ , that we assume increasing, and the yield factor  $k_i$ . Assume that for each  $i$ ,  $\mu_i(s_{in}) > D$ , which is a necessary condition for the existence of a positive equilibrium for each species alone. It is well known that under this condition [18] the equilibrium  $(0, \dots, 0, x_{i*}, 0, \dots, 0)$ , where  $x_{i*} = \min_i \mu_i^{-1}(D)$ , is globally asymptotically stable. This means that all species except one are eliminated [10]. Although this result has been validated through some laboratory experiments [9], coexistence of several species is observed in complex or real world applications (such as continuously stirred bioreactors). Later on, several extensions of this model have been proposed in the literature, exhibiting the existence of a strictly positive asymptotically stable equilibrium. Among them, let us mention time-varying nutrient feed [19,11,8,3], multi-resource models [13,12] turbidity operating conditions [5] or crowding effects [4]. In this note, we show that the mere consideration of an intra-specific dependency of the growth functions is enough to explain a possible coexistence. In the basic model (5), we replace the functions  $\mu_i$  of  $s$  by functions  $h_i$  of  $s$  and  $x_i$

$$\begin{aligned} \dot{s} &= - \sum_{j=1}^n \frac{h_j(s, x_j)}{k_j} x_j + D(s_{in} - s), \\ \dot{x}_i &= x_i(h_i(s, x_i) - D) \quad (i = 1, \dots, n) \end{aligned} \tag{6}$$

with the following hypotheses. For all  $i = 1, \dots, n$ ,

- H5. The functions  $h_i$  are  $C^1$  with  $\frac{\partial h_i}{\partial s} > 0$  and  $\frac{\partial h_i}{\partial x_i}(s, \cdot) < 0$  for  $s > 0$ ,  $h_i(0, \cdot) = 0$ . For  $s > 0$  and  $x_i \in \mathbb{R}_+$ ,  $h_i(s, x_i) > 0$ .
- H6. The inequality  $h_i(s_{in}, 0) > D$  holds.
- H7. For any  $s \geq 0$ ,  $\lim_{x_i \rightarrow +\infty} h_i(s, x_i) = 0$ .

For instance,  $h_i$  could be of the form  $h_i(s, x_i) = \mu_i(s)g_i(x_i)$ , where  $g_i$  is a decreasing positive function with  $g_i(0) = 1$  and going to zero when its argument goes to  $+\infty$ . Another example is provided by ratio-dependent growth rate functions  $f_i(x_i, u) = \mu_i(u/x_i)$ . These examples will be studied in details in a paper in preparation [14].

By taking the derivative along the trajectories of  $z = s - s_{in} + \sum_{i=1}^n x_i/k_i$ , one obtains  $\dot{z} = -Dz$ . The solutions  $x(\cdot)$  of (6) are then solutions of a non-autonomous system of the form (1) with

$$f_i(x_i, u) = h_i(s_{in} + u, x_i) - D$$

and the feedback

$$u(t, x) = -g(t, x) = z(0) e^{-Dt} - \sum_{i=1}^n \frac{x_i}{k_i}.$$

For this choice of functions  $f_i$ ,  $g$ , Assumptions H1 and H2 are induced by Assumptions H5 and H6, while H3 is trivially fulfilled with

$$r(x) = \sum_{i=1}^n \frac{x_i}{k_i}.$$

Finally, it can be easily shown that Assumption H4 is satisfied if and only if

$$\tilde{u} < -r(\varphi_1(\tilde{u}), \dots, \varphi_n(\tilde{u})) \quad \text{with } \tilde{u} = \max_i \psi_i(0).$$

Then, there exists a unique equilibrium  $x^* \in \mathcal{P}$  such that  $x_i^* = \varphi_i(u^*)$  for any  $i$ , with  $u^* = -r(x^*)$ . According to Proposition 2.1, the equilibrium  $x^*$  is globally asymptotically stable on  $\mathcal{P}$ .

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