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RÉSUMÉ. On considère un modèle de compétition de Lotka-Volterra de deux espèces dans un environnement variable. On utilise la théorie de la moyennisation, ainsi que la théorie de Floquet pour montrer que des fluctuations périodiques entre deux environnements qui sont tous les deux favorables pour l'une des espèces peuvent conduire à l'extinction de cette espèce ou bien à la coexistence des deux espèces.

ABSTRACT. We consider two dimensional Lotka-Volterra systems in fluctuating environment. Using averaging and Floquet theory, we show that periodic switching between two environments both favorable to the same species can lead to the extinction of this species or coexistence of the species.

MOTS-CLÉS : Dynamique des populations, coexistence, moyennisation, exclusion compétitive, théorie de Floquet

KEYWORDS : Population dynamics, coexistence, Averaging, competitive exclusion, Floquet theory

1. Introduction

In ecology, the principle of competitive exclusion formulated by Gause [7] and Hardin [8], asserts that when two species compete with each other for the same resource, the "better" competitor will eventually exclude the other. However the observed diversity of certain communities is in apparent contradiction with this principle. As a solution to this paradox, Hutchinson [9] suggested that sufficiently frequent variations of the environment can keep species abundances away from the equilibrium points predicted by competitive exclusion. The idea that temporal fluctuations of the environment can reverse the trend of competitive exclusion has been widely explored in the ecology literature. See [2, 3] for an overview and further references. Our goal here is to investigate rigorously this phenomenon for a two-species Lotka-Volterra model of competition under the assumption that the environment (defined by the parameters of the model) fluctuates periodically between two environments that are both favorable to the same species. We will precisely describe the range of possible behaviors and explain why counter-intuitive behaviors, including coexistence of the two species, or extinction of the species favored by the environments, can occur.

2. Lotka-Volterra model of competition

The Lotka-Volterra model of competition of two species of abundances x and y is

$$\begin{aligned} \dot{x} &= rx\,(1 - ax - by) \\ \dot{y} &= sy\,(1 - cx - dy) \end{aligned} \tag{1}$$

where r and s are the intrinsic growth rates of species x and y and a and d are the intra specific competition coefficients and b and c are the inter specific competition coefficients. The environment is characterized by the growth rates r and s and the matrix of competition coefficients

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$

Beside the boundary equilibria $E_0 = (0, 0)$, $E_1 = (1/a, 0)$, and $E_2 = (0, 1/d)$, the system can have a non trivial equilibrium

$$E_3 = \left(\frac{d-b}{ad-bc}, \frac{a-c}{ad-bc} \right)$$

Only nonnegative equilibria are of interest.

It is well known (see, e.g. [12]) that 4 cases can be obtained, see Figure 1 :

– Case (i) : if $a > c$ and $b < d$ then there is coexistence, that is all solutions converge toward the positive equilibrium E_3, see Figure 1(i).

– Case (ii) : if $a < c$ and $b < d$ then species 1 wins the competition, that is all solutions converge toward the equilibrium E_1, see Figure 1(ii). We say that the environment is bad for species 2 (or good for species 1).

– Case (iii) : if $a > c$ and $b > d$ then species 2 wins the competition, that is all solutions converge toward the equilibrium E_2, see Figure 1(iii). We say that the environment is bad for species 1 (or good for species 2).

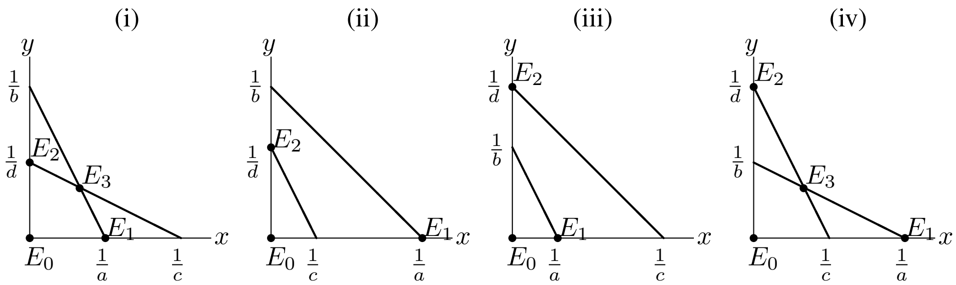

Figure 1. *The isoclines $\dot{x} = 0$ and $\dot{y} = 0$: (i) coexistence, (ii) species 1 wins, (iii) species 2 wins , (iv) bistability.*

– Case (iv) : if $a < c$ and $b > d$ then there is bistability, that is equilibria E_1 and E_2 are both stable, and their basin of attraction are separated by the stables manifolds of the positive equilibrium E_3 which is a saddle point, see Figure 1(iv).
We assume now that the environment has two alternating seasons with period T, a first season corresponding to proportion α_1 of the time, $\alpha_1 \in [0, 1]$, characterized by environment

$$r_1, \quad s_1, \quad A_1 = \begin{pmatrix} a_1 & b_1 \\ c_1 & d_1 \end{pmatrix} \tag{2}$$

and a second season corresponding to proportion α_2 of the time, ($\alpha_2 = 1 - \alpha_1$) characterized by environment

$$r_2, \quad s_2, \quad A_2 = \begin{pmatrix} a_2 & b_2 \\ c_2 & d_2 \end{pmatrix}. \tag{3}$$

We assume that both environments are bad for species 1, that is

$$a_1 > c_1, \quad b_1 > d_1, \quad a_2 > c_2, \quad b_2 > d_2 \tag{4}$$

Let $N_0 = \{0, 1, \ldots\}$. For $n \in N_0$, the growth of the species is given by the following periodic system :

$$\begin{cases} \dot{x} = r_1 x(1 - a_1 x - b_1 y) \\ \dot{y} = s_1 y(1 - c_1 x - d_1 y) \end{cases} \quad \text{if } t \in [nT, nT + \alpha_1 T)$$
$$\begin{cases} \dot{x} = r_2 x(1 - a_2 x - b_2 y) \\ \dot{y} = s_2 y(1 - c_2 x - d_2 y) \end{cases} \quad \text{if } t \in [nT + \alpha_1 T, (n+1)T) \tag{5}$$

For the general theory of periodic Lotka-Volterra systems, the reader is referred to [4, 5, 6]. Our purpose is to describe the behaviour of the periodic system (5) and to give the conditions on the parameters such that the species 1 is persistent, that is to say, the fluctuations between the two bad environments for species 1 is good for that species.

2.1. T very small : averaging

When T is very small, local stability of the origin of (5) can be characterized using averaging theory. In this case the solutions of (5) are approximated by the solutions of the averaged system, see Appendix B.1:

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \alpha_1 \begin{pmatrix} r_1 x(1 - a_1 x - b_1 y) \\ s_1 y(1 - c_1 x - d_1 y) \end{pmatrix} + \alpha_2 \begin{pmatrix} r_2 x(1 - a_2 x - b_2 y) \\ s_2 y(1 - c_2 x - d_2 y) \end{pmatrix}$$

that is to say

$$\begin{aligned} \dot{x} &= \overline{r}x\left(1-\overline{a}x-\overline{b}y\right) \\ \dot{y} &= \overline{s}y\left(1-\overline{c}x-\overline{d}y\right) \end{aligned} \tag{6}$$

where

$$\overline{r}=\alpha_1 r_1+\alpha_2 r_2, \quad \overline{a}=\frac{\alpha_1 r_1 a_1+\alpha_2 r_2 a_2}{\alpha_1 r_1+\alpha_2 r_2}, \quad \overline{b}=\frac{\alpha_1 r_1 b_1+\alpha_2 r_2 b_2}{\alpha_1 r_1+\alpha_2 r_2}$$

$$\overline{s}=\alpha_1 s_1+\alpha_2 s_2, \quad \overline{c}=\frac{\alpha_1 s_1 c_1+\alpha_2 s_2 c_2}{\alpha_1 s_1+\alpha_2 s_2}, \quad \overline{d}=\frac{\alpha_1 s_1 d_1+\alpha_2 s_2 d_2}{\alpha_1 s_1+\alpha_2 s_2}$$

The fluctuating environment is good for specie 1 if and only if :

$$\overline{a}<\overline{c}, \quad \overline{b}<\overline{d} \tag{7}$$

The condition $\overline{a}<\overline{c}$ is equivalent to

$$I_1\alpha_1^2+I_2\alpha_2^2-J\alpha_1\alpha_2<0 \tag{8}$$

where

$$I_1=r_1s_1(a_1-c_1), \quad I_2=r_2s_2(a_2-c_2), \quad J=r_1s_2(c_2-a_1)+r_2s_1(c_1-a_2)$$

The inequality $\overline{b}<\overline{d}$ is equivalent to the following

$$K_1\alpha_1^2+K_2\alpha_2^2-L\alpha_1\alpha_2<0 \tag{9}$$

where

$$K_1=r_1s_1(b_1-d_1), \quad K_2=r_2s_2(b_2-d_2), \quad L=r_1s_2(b_1-d_2)+r_2s_1(b_2-d_1)$$

Therefore, using the condition (4), we see that for α_1 close to 0 (that is α_2 close to 1) or α_1 close to 1 (that is α_2 close to 0), (8) and (9) are not satisfied, and hence the averaged environment (6) is bad for species 1. But what happens when α is not close to 0 or 1 ? For instance, for the following bad for species 1 environments

$$r_1=5, \quad s_1=1, \quad A_1=\begin{pmatrix} 1/2 & 1/2 \\ 1/3 & 1/3 \end{pmatrix} \tag{10}$$

$$r_2=1, \quad s_2=5, \quad A_2=\begin{pmatrix} 2 & 2 \\ 1 & 1 \end{pmatrix} \tag{11}$$

it was noticed [10] that for $\alpha_1=0.5$, the fluctuating environment is good for species 1. Indeed, in this case we have

$$\overline{r}=\overline{s}=3, \quad \overline{A}=\begin{pmatrix} 3/4 & 3/4 \\ 8/9 & 8/9 \end{pmatrix}$$

Hence $\overline{a}<\overline{c}$, $\overline{b}<\overline{d}$, so that the fluctuating environment is good for species 1. This phenomenon corresponds to the paradoxical situation where species 1 disappears in two distinct environments, but wins the competition in a periodical fluctuation of these two bad environments, see Figure 2.

Let us determine more precisely the range of α_1 for which the fluctuating environment is good for species 1. We have the following result.

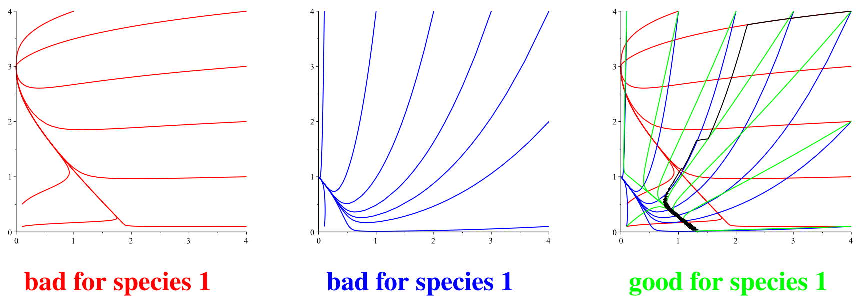

Figure 2. *The fluctuation of the two bad for species 1 environments corresponding to (10-11) is a good environment for species 1. The solution of the fluctuating environment of initial condition* $(4, 4)$ *(in black) is approximated by a solution of the averaged environment (in green).*

Proposition 2.1 *Assume that the environments (2) and (3) are bad for species 1, that is to say (4) holds. Assume that* $J > 2\sqrt{I_1 I_2}$ *and* $L > 2\sqrt{K_1 K_2}$. *For* T *sufficiently small, the fluctuation environment (5) is good for species 1 when* $\max(\alpha_-, \alpha^-) + \epsilon < \alpha_1 < \min(\alpha_+, \alpha^+) - \epsilon$ *with* ϵ *small enough, where* α_-, α_+ α^- *and* α^+ *are given by:*

$$\alpha_- = \frac{2I_2 + J - \sqrt{J^2 - 4I_1 I_2}}{2(I_1 + I_2 + J)}, \qquad \alpha_+ = \frac{2I_2 + J + \sqrt{J^2 - 4I_1 I_2}}{2(I_1 + I_2 - J)},$$

$$\alpha^- = \frac{2K_2 + L - \sqrt{L^2 - 4K_1 K_2}}{2(K_1 + K_2 + L)}, \qquad \alpha^+ = \frac{2K_2 - L + \sqrt{L^2 - 4K_1 K_2}}{2(K_1 + K_2 + L)}.$$

Proof. The proof is given in Appendix A.1

For the parameter values (10-11) we have

$$\alpha_- = \alpha^- = \frac{5}{8} - \frac{1}{40}\sqrt{145} \approx 0.32, \quad , \alpha_+ = \alpha^+ = \frac{5}{8} + \frac{1}{40}\sqrt{145} \approx 0.92$$

Therefore, for T small enough, the fluctuating environment is good for species 1 for $0.32 < \alpha_1 < 0.92$.

2.2. T not very small : Floquet theory

What happens if T is not very small ? We performed numerical simulations with the parameter values (10-11), $\alpha_1 = 0.5$ and $T = 1$, $T = 2$ and $T = 4$ respectively, see Figure 3. We see on the numerical simulation that the fluctuating environment is good for species 1 for $T = 1$ and bad for $T = 4$, and both species coexist if $T = 2$.

The study of the system for values of T that are not very small is obtained by the Floquet theory. Indeed the local stability of the origin of the switching system (5) can be characterized using the Floquet monodromy matrix, see Appendix B.2.

The periodic system (5) has two periodic solutions lying on the invariant sets $x = 0$ and $y = 0$. These periodic solutions can be computed explicitly and their stability properties are determined using the Floquet theory.

On $y = 0$, (5) reduces to the scalar periodic system

$$\left\{ \begin{array}{ll} \dot{x} = r_1 x(1 - a_1 x) & \text{if } t \in [nT, nT + \alpha_1 T) \\ \dot{x} = r_2 x(1 - a_2 x) & \text{if } t \in [nT + \alpha_1 T, (n+1)T) \end{array} \right. \tag{12}$$

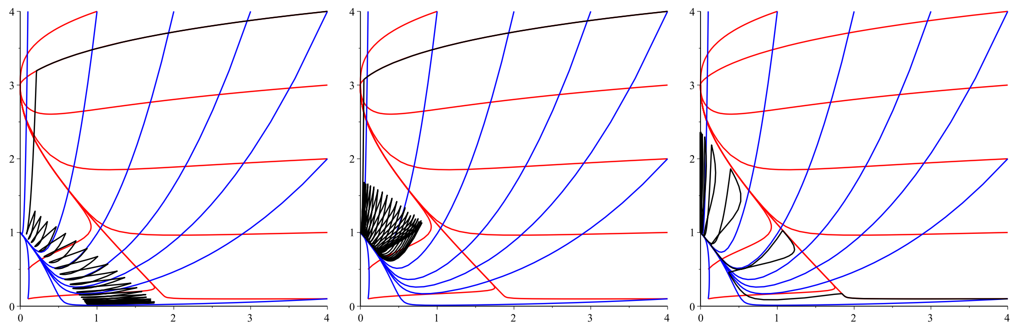

Figure 3. *On the left, a solution with initial condition $(4,4)$ and $T = 1$: the fluctuating environment is good for species 1. On the center, a solution with initial condition $(4,4)$ and $T = 2$: the fluctuating environment is good for both species. On the right, a solution with initial condition $(4, 0.1)$ and $T = 4$: the fluctuating environment is bad for species 1.*

The solution of this system, with initial condition $x(0) = x_0$ is given by

$$x(t) = \begin{cases} \frac{x_0 e^{r_1 t}}{1+a_1 x_0 [e^{r_1 t}-1]} & \text{if } t \in [0, \alpha_1 T) \\ \\ \frac{x_1 e^{r_2(t-\alpha_1 T)}}{1+a_2 x_1 \left[e^{r_2(t-\alpha_1 T)}-1\right]} & \text{if } t \in [\alpha_1 T, T) \end{cases} \tag{13}$$

where

$$x_1 = x(\alpha_1 T) = \frac{x_0 e^{r_1 \alpha_1 T}}{1 + a_1 x_0 \left[e^{r_1 \alpha_1 T} - 1\right]} \tag{14}$$

This solution is periodic if and only if $x(T) = x_0$, which is an algebraic equation in x_0 admitting the solution $x_0 = 0$ corresponding to the trivial periodic solution $x(t) = 0$ and the positive solution

$$x_0 = \frac{e^{[r_1\alpha_1 + r_2\alpha_2]T} - 1}{a_1\left(e^{r_1\alpha_1 T} - 1\right) + a_2 e^{r_1\alpha_1 T}\left(e^{r_2\alpha_2 T} - 1\right)} \tag{15}$$

corresponding to a non trivial positive solution $x = p(t)$. Let $(p(t), 0)$ be the corresponding periodic solution of (5).

Proposition 2.2 *The necessary and sufficient condition on α_1 and T such that $(p(t), 0)$ is stable is $\lambda < 0$, where λ is given explicitly by*

$$\lambda = L_1(x_1) - L_1(x_0) + L_2(x_0) - L_2(x_1),$$

where

$$L_i(x) = \frac{s_i}{r_i}\left(\ln(x) + \frac{c_i - a_i}{a_i}\ln(1 - a_i x)\right).$$

Proof. The proof is given in Appendix A.2

Similarly, on $x = 0$, (5) reduces to the scalar periodic system

$$\begin{cases} \dot{y} = s_1 y(1 - d_1 y) & \text{if } t \in [nT, nT + \alpha_1 T) \\ \dot{y} = s_2 y(1 - d_2 y) & \text{if } t \in [nT + \alpha_1 T, (n+1)T) \end{cases} \tag{16}$$

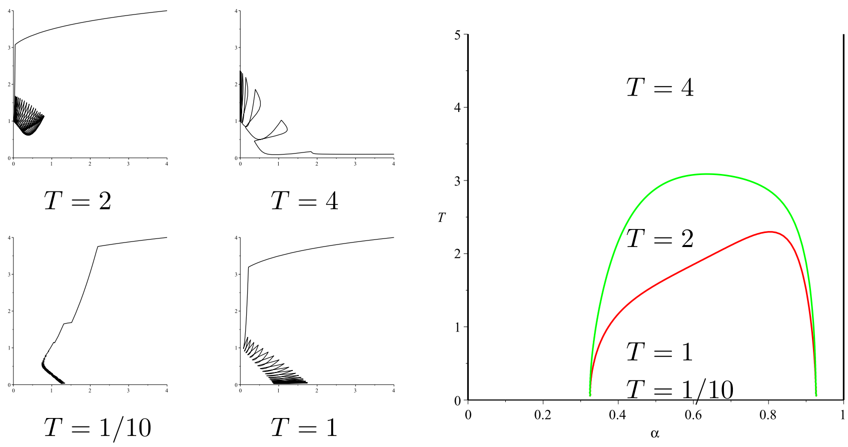

Figure 4. *The set of points where $\lambda = 0$ (in red) and $\mu = 0$ (in green) with respect of T and $\alpha_1 = \alpha$. If $\alpha = 0.5$, then for $T = 0.1$ or $T = 1$, the fluctuating environment is good for species 1, and bad for species 2; For $T = 2$, the fluctuating environment is good for both species; For $T = 4$, the fluctuating environment is good for species 2, and bad for species 1.*

This system has a a non trivial positive solution $y = q(t)$ of initial condition

$$y_0 = \frac{e^{[s_1\alpha_1 + s_2\alpha_2]T} - 1}{d_1\left(e^{s_1\alpha_1 T} - 1\right) + d_2 e^{s_1\alpha_1 T}\left(e^{s_2\alpha_2 T} - 1\right)} \tag{17}$$

Proposition 2.3 *The necessary and sufficient condition on α_1 and T such that $(0, q(t))$ is stable is $\mu < 0$, where μ is given by*

$$\mu = M_1(y_1) - M_1(y_0) + M_2(y_0) - M_2(y_1)$$

where

$$M_i(y) = \frac{r_i}{s_i}\left(\ln(y) + \frac{b_i - d_i}{d_i}\ln(1 - d_i y)\right).$$

Proof. The proof is given in Appendix A.3

Using Maple we can plot the curves in the plane (α_1, T) defined by $\lambda = 0$ and $\mu = 0$. for the parameters values (10-11), see Figure 4. Recall that both environments given by (10-11) are bad for species 1. The picture shows that:

– If (α_1, T) is below the red curve, for instance for $(\alpha_1 = 0.5, T = 1/10)$ or $(\alpha_1 = 0.5, T = 1)$, then we have $\lambda < 0$ and $\mu > 0$, and hence the fluctuating environment is good for species 1, and bad for species 2.

– If (α_1, T) is above the red curve and below the green curve, for instance for $(\alpha_1 = 0.5, T = 2)$, then we have $\lambda > 0$ and $\mu > 0$, and hence the fluctuating environment is good for both species, that is to say the system exhibits coexistence.

– If (α_1, T) is above the green curve, for instance for $(\alpha_1 = 0.5, T = 4)$, then we have $\lambda > 0$ and $\mu < 0$, hence the fluctuating environment is good for species 2 and bad for species 1.

3. Conclusion

Our study has shown that the fluctuations between two environments that are both bad for one species (the population goes to extinction for this environment) can lead to the growth of this species. Similarly, the fluctuations between two environments that are both good for one species (the population is persistent for this environment) can lead to the extinction of this species. These behaviours are not exceptional and can hold for a large set of values of parameters. Averaging theory and Floquet theory are useful tools for these studies. The results of this paper extend to the stochastic case of random switching [1]: relying on results on stochastic persistence and piecewise deterministic Markov processes, it was shown that random switching between two environments that are both favorable to the same species can lead to the extinction of this species or coexistence of the two competing species.

A. Proofs

A.1. Proof of Proposition 2.1

The condition $\overline{a} < \overline{c}$ is equivalent to the condition (8). Using that $\alpha_2 = 1 - \alpha_1$ this condition is a second order inequality in α_1. By straightforward calculations we see that there exists $\alpha_1 \in (0,1)$ such that (8) holds, if and only if the following condition is satisfied

$$J > 2\sqrt{I_1 I_2}$$

In this case the condition $\overline{a} < \overline{c}$ is satisfied if and only if $\alpha_- < \alpha_1 < \alpha_+$, where α_- and α_+ are defined as in the proposition.

Similarly by straightforward calculations we see that there exists $\alpha_1 \in (0,1)$ such that (9) holds, if and only if the following condition is satisfied

$$L > 2\sqrt{K_1 K_2}$$

In this case, the condition $\overline{b} < \overline{d}$ is satisfied if and only if $\alpha^- < \alpha_1 < \alpha^+$, where α^- and α^+ are defined as in the proposition.

A.2. Proof of Proposition 2.2

The variational equation of (5) around the periodic solution $(p(t), 0)$ takes the form

$$\begin{cases} \dot{x} = r_1(1 - 2a_1 p(t))x - r_1 b_1 p(t) y \\ \dot{y} = s_1(1 - c_1 p(t)) y \end{cases} \quad \text{if } t \in [nT, nT + \alpha_1 T)$$

$$\begin{cases} \dot{x} = r_2(1 - 2a_2 p(t))x - r_2 b_2 p(t) y \\ \dot{y} = s_2(1 - c_2 p(t)) y \end{cases} \quad \text{if } t \in [nT + \alpha_1 T, (n+1)T)$$

This triangular system can be solved explicitly. The computations are straightforward and show that the characteristic multiplier corresponding to x is always less than 1. The y component of the solution is given by

$$y(t) = \begin{cases} y(0) e^{\int_0^t s_1(1 - c_1 p(\tau)) d\tau} & \text{if } t \in [0, \alpha_1 T) \\ \\ y(\alpha_1 T) e^{\int_{\alpha_1 T}^t s_2(1 - c_2 p(\tau)) d\tau} & \text{if } t \in [\alpha_1 T, T) \end{cases}$$

Therefore the characteristic exponent λ, defined by $y(T) = y(0)e^{\lambda}$ is given by

$$\lambda = \int_0^{\alpha_1 T} s_1(1 - c_1 p(\tau))d\tau + \int_{\alpha_1 T}^{T} s_2(1 - c_2 p(\tau))d\tau$$

Using the fact that $p(t)$ is the solution of (12), the change of variable $x = p(\tau)$ is these integrals gives

$$\lambda = \int_{x_0}^{x_1} \frac{s_1(1 - c_1 x)}{r_1 x(1 - a_1 x)}dx + \int_{x_1}^{x_0} \frac{s_2(1 - c_2 x)}{r_2 x(1 - a_2 x)}dx$$

where x_0 and x_1 are given by (15) and (14) respectively. Hence λ is given explicitly by

$$\lambda = L_1(x_1) - L_1(x_0) + L_2(x_0) - L_2(x_1)$$

where

$$L_i(x) = \frac{s_i}{r_i}\left(\ln(x) + \frac{c_i - a_i}{a_i}\ln(1 - a_i x)\right)$$

is a primitive of $\frac{s_i(1-c_i x)}{r_i x(1-a_i x)}$.

A.3. Proof of Proposition 2.3

The variational equation of (5) around the periodic solution $(0, q(t))$ takes the form

$$\begin{cases} \dot{x} = r_1(1 - b_1 q(t))x \\ \dot{y} = -s_1 c_1 q(t)x + s_1(1 - 2d_1 q(t))y \end{cases} \quad \text{if } t \in [nT, nT + \alpha_1 T)$$
$$\begin{cases} \dot{x} = r_2(1 - b_2 q(t))x \\ \dot{y} = -s_2 c_2 q(t)x + s_2(1 - 2d_2 q(t))y \end{cases} \quad \text{if } t \in [nT + \alpha_1 T, (n+1)T)$$

The characteristic multiplier corresponding to y is always less than 1 and the characteristic exponent μ, defined by $x(T) = x(0)e^{\mu}$ is given by

$$\mu = \int_{y_0}^{y_1} \frac{r_1(1 - b_1 y)}{s_1 y(1 - d_1 y)}dy + \int_{y_1}^{y_0} \frac{r_2(1 - b_2 y)}{s_2 y(1 - d_2 y)}dy$$

where y_0 is given by (17) and

$$y_1 = q(\alpha_1 T) = \frac{y_0 e^{s_1 \alpha_1 T}}{1 + d_1 y_0 \left[e^{s_1 \alpha_1 T} - 1\right]}$$

Hence μ is given explicitly by

$$\mu = M_1(y_1) - M_1(y_0) + M_2(y_0) - M_2(y_1)$$

where

$$M_i(x) = \frac{r_i}{s_i}\left(\ln(y) + \frac{b_i - d_i}{d_i}\ln(1 - d_i y)\right)$$

is a primitive of $\frac{r_i(1-b_i y)}{s_i y(1-d_i y)}$.

B. Tools

B.1. Averaging

Let $f(t,x)$ be a periodic function in t. We assume that the period is 1. Let $T > 0$, small enough. The purpose of averaging theory is to describe the solutions of the T-periodic differential equation

$$\dot{x} = f\left(\frac{t}{T}, x\right)$$

More precisely, the solutions are approximated by the solutions of the averaged equation

$$\dot{x} = \overline{f}(x)$$

where $\overline{f}(x) = \int_0^1 f(t,x)dt$ is the mean value of f [11].

B.2. Floquet theory

Consider the linear time varying system

$$\left\{ \begin{array}{l} \dot{x}(t) = A(t)x(t) \\ x(0) = x_0 \end{array} \right. \tag{18}$$

where $x(t) \in R^n$ the function $t \mapsto A(t) \in R^{n\times n}$ is piecewise continuous, bounded, and periodic with period T. Although its parameters $A(t)$ vary periodically, the solutions of (18) are typically not periodic, and despite its linearity, closed form solutions of (18) typically cannot be found. We denote by $\Phi(t)$ the fundamental matrix solution

$$\left\{ \begin{array}{l} \dot{\Phi}(t) = A(t)\Phi(t) \\ \Phi(0) = I \end{array} \right. .$$

The matrix $M = \Phi(T)$ is called monodromy matrix and the ρ_i eigenvalues of M are called characteristic or Floquet exponents. The zero equilibrium is stable if all Floquet exponents have module less than 1 or, the spectral radius of M being less than 1. If there is a Floquet exponent with a module greater than 1 (equivalent to the spectral radius of M is greater than one), then the zero equilibrium is unstable.

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