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A note on the stability of periodic orbits of planar Lotka–Volterra systems

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Abstract. In this paper we revisit previous results in the literature dealing with the stability of periodic solutions of periodic predator–prey Lotka–Volterra systems. These results provide stability criteria for the periodic orbits based on boundaries for the average of the coexistence states. In the way it was presented, these boundaries are independent of each other and thus provide a very practical sufficient condition for asymptotic stability. In this note we prove that this independent boundaries can be refined into an intertwined boundary, providing a more sharp sufficient condition.

Keywords: Lotka–Volterra systems, population dynamics, predator–prey model.

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1 Introduction

Consider the planar non-autonomous periodic Lotka-–Volterra system given by

$$\dot{u} = u(a(t) - b(t)u - c(t)v), \quad \dot{v} = v(d(t) + e(t)u - f(t)v), \tag{1.1}$$

with continuous and T-periodic coefficients, $T > 0$. Suppose that b, c, e and f are strictly positive functions. Under these conditions (1.1) models in the positive quadrant $\mathbb{R}^2_+ = \{(u, v) \in \mathbb{R}^2 \colon u > 0,\ v > 0\}$ a predator-prey interaction between two species in a T-periodic environment. In the last decades, there is a great effort of R. Ortega and coauthors for the understanding of the T-periodic orbits of (1.1). In what follows, we present a brief survey on the obtained results. System (1.1) can have three types T-periodic non-negative solutions $(u(t), v(t))$.

(a) The *trivial state*, given by $u(t) = v(t) = 0$ for every $t \in [0, T]$;

(b) The *semi-trivial state*, given by:

  (i) $u(t) > 0$, $v(t) = 0$ for every $t \in [0, T]$, or

  (ii) $u(t) = 0$, $v(t) > 0$ for every $t \in [0, T]$;

(c) The *coexistence state*, given by $u(t) > 0$ and $v(t) > 0$ for every $t \in [0, T]$.

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Observe that the trivial and semi-trivial states represents the extinction of at least one of the species. The question about the *existence* of coexistence states was completely solved by the authors in [4]. More precisely, let

$$\lambda = \frac{1}{T}\int_0^T a, \quad \mu = \frac{1}{T}\int_0^T d.$$

It follows from [4] that (1.1) has a semi-trivial state of type (i) (resp. (ii)) if, and only if, $\lambda > 0$ (resp, $\mu > 0$). Moreover, in this case the semi-trivial state $(\theta_\lambda(t), 0)$ (resp. $(0, \theta_\mu(t))$ is given by the unique positive T-periodic solution of

$$\dot{u} = u(a(t) - b(t)u) \quad \big(\text{resp. } \dot{v} = v(d(t) - f(t)v)\big).$$

In particular, if it exists then it is unique (of its type). From [4, Section 4] we have that the following statements hold (for the definition of *linear* and *asymptotic* stability, see Appendix A).

(a) The trivial state $(0,0)$ is linearly stable if, and only if, $\lambda \leqslant 0$ and $\mu \leqslant 0$. Moreover, in this case it is also asymptotically stable in $\mathbb{R}^2_+$.

(b) The semi-trivial state $(\theta_\lambda, 0)$ is linearly stable if, and only if, $\lambda > 0$ and

$$\mu \leqslant -\frac{1}{T}\int_0^T e\theta_\lambda.$$

Moreover, in this case it is also asymptotically stable in $\mathbb{R}^2_+$.

(c) The semi-trivial state $(0, \theta_\mu)$ is linearly stable if, and only if, $\mu > 0$ and

$$\lambda \leqslant \frac{1}{T}\int_0^T c\theta_\mu.$$

Moreover, in this case it is also asymptotically stable in $\mathbb{R}^2_+$.

It can be proved [4, Theorem 4.1] that for a coexistence state to exist it is necessary to the trivial and semi-trivial states (when they exist) to be linearly unstable. That is, it is necessary

$$\mu > -\frac{1}{T}\int_0^T e\theta_\lambda, \quad \lambda > \frac{1}{T}\int_0^T c\theta_\mu. \tag{1.2}$$

On the other hand, it also follows from [4, Section 5] that (1.2) is as well a sufficient condition and thus we have a complete characterization on the existence of coexistence states for system (1.1). Moreover, it follows from [4, Theorem 5.1] that system (1.1) always has at most a finite number of coexistence states. With the existence completely characterized, the question turned to the finiteness, uniqueness and stability of the coexistence states. For this end, before we enunciate the obtained results, we introduce some technical notations.

Let $\mathbb{T}_T = \mathbb{R}/T\mathbb{Z}$ be endowed with the push-forward measure of the Lebesgue measure on $\mathbb{R}$ (see Bogachev [2, Section 3.6]). That is, the measure σ such that $\sigma(a,b) = b - a$, for $0 \leqslant a \leqslant b \leqslant T$. Given $p \in [1, \infty]$, let $L^p = L^p(\mathbb{T}_T)$ denote the usual Lebesgue L^p-space associated with $\mathbb{T}_T$. Since $\mathbb{T}_T$ has finite measure, we observe that

$$L^\infty \subset L^{p_2} \subset L^{p_1} \subset L^1,$$

where $1 \leqslant p_1 \leqslant p_2 \leqslant \infty$.

In particular, since the coefficients of (1.1) are continuous, it follows that they lie in L^∞ and thus also in L^p, for every $p \in [1,\infty]$. Let $\varphi \in L^p$. For simplicity we denote $\|\varphi\|_p = \|\varphi\|_{L^p}$, where $\|\cdot\|_{L^p}$ is the usual norm of the Banach space L^p. Let also

$$\varphi_L = \min_{t\in[0,T]}\{\varphi(t)\}, \quad \varphi_M = \max_{t\in[0,T]}\{\varphi(t)\}, \quad \overline{\varphi} = \frac{1}{T}\int_0^T \varphi,$$

be the minimum, maximum and average of φ. About the uniqueness of the coexistence states of (1.1), consider the statements

$$\overline{a} > 0, \quad -\left(\frac{e}{b}\right)_L < \frac{\overline{d}}{\overline{a}} < \left(\frac{f}{c}\right)_L, \tag{1.3}$$

and

$$\left(\frac{b}{e}\right)_L > \left(\frac{c}{f}\right)_M. \tag{1.4}$$

The authors in [1] proved that if (1.4) holds, then (1.1) has at most one coexistence state [1, Proposition 3.3]. As observed by the authors in [1, Remark 2, p. 11], if both (1.3) and (1.4) holds, then it follows from Tineo [8, Theorem 1.5] that (1.1) has exactly one coexistence state and it is *globally* asymptotically stable.

More sufficient conditions for asymptotically stability of coexistence states were obtained by R. Ortega and coauthors [1,5]. Such conditions can somewhat be called L_1*-condition* and L_∞*-condition* (see Remarks 2.3 and 2.4). In recent years V. Ortega and Rebelo [6] constructed a bridge between these two conditions, obtaining a L_p*-condition*, $p \in [1,\infty]$. Such condition requires that the L_p-norm of all possible coexistence states (u_0, v_0) to satisfy a given inequality. To this end, the authors in [6] also provide upper bounds for $\|u_0\|_p$ and $\|v_0\|_p$, independent from each other. This independence provides a *unified* sufficient condition for uniqueness and asymptotically stability of (u_0, v_0).

In this paper we obtain new *intertwined* upper bounds for $\|u_0\|_p$ and $\|v_0\|_p$, which in turn imply on new sufficient conditions for uniqueness and asymptotically stability of (u_0, v_0), that can be applied when the unified test is inconclusive. The paper is organized as follows. In Section 2 we state our main Theorem. At Section 3 we have some preliminary results to prove the main Theorem at Section 4. In Section 5 we provide an example where previous results in the literature are inconclusive, while ours is not. We also provide some further thoughts. Finally, we have an Appendix with some technicalities and illustrations.

2 Statement of the main result

Given $p \in [1,\infty)$ and $\varphi \in L^p$ non-negative, the L^p*-average* $\overline{\varphi}_p \in \mathbb{R}_{\geqslant 0}$ is given by,

$$\overline{\varphi}_p = \frac{1}{T^{\frac{1}{p}}}\left(\int_0^T \varphi^p\right)^{\frac{1}{p}} = \frac{1}{T^{\frac{1}{p}}}\|\varphi\|_p.$$

If $p = \infty$, then we define $\overline{\varphi}_\infty = \|\varphi\|_\infty$. Observe that $\overline{\varphi}_p \to \overline{\varphi}_\infty$ as $p \to \infty$.

Given a system of the form (1.1) and $p \in [1,\infty)$, let $C_p \subset \mathbb{R}^2$ be the set given by the points $(x,y) \in \mathbb{R}^2$ such that $x > 0$, $y > 0$ and

$$\begin{aligned} b_L U^{1-p} x^p + c_L V^{1-p} y^p \leqslant \overline{a} \leqslant b_M x + c_M y \\ -e_M x + f_L V^{1-p} y^p \leqslant \overline{d} \leqslant -e_L U^{1-p} x^p + f_M y, \end{aligned} \tag{2.1}$$

where,

$$U = \left(\frac{a}{b}\right)_M, \quad V = \left(\frac{d}{f}\right)_M + \left(\frac{e}{f}\right)_M U.$$

Let also $C_\infty \subset \mathbb{R}^2$ be the set given by

$$0 < x \leqslant U, \quad 0 < y \leqslant V.$$

For an illustration of C_p and more details about the definition of C_∞, see Appendix B. We observe that C_p is bounded and that it may be empty. Let also $\mathcal{J} \colon [1,\infty) \to \mathbb{R}$ be given by,

$$\mathcal{J}(q) = \int_0^{2\pi} \frac{1}{\left(|\cos\theta|^{2q} + |\sin\theta|^{2q}\right)^{\frac{1}{q}}}\, d\theta.$$

It follows from [6, Proposition 2.2] that,

$$\lim_{q\to\infty} \mathcal{J}(q) = 8.$$

Hence, we can continuously extend $\mathcal{J}$ to $[1,\infty]$ by defining $\mathcal{J}(\infty) = 8$. For more details about $\mathcal{J}(q)$, see Appendix C. Given $p \in [1,\infty]$, we recall that its *conjugate* $q \in [1,\infty]$ is given by the unique solution of $1/p + 1/q = 1$. In what follows q always denote the conjugate of p. Our main result is the following.

Theorem 2.1. *Consider a system of the form (1.1) and its respective set C_p, $p \in [1,\infty]$. Then the following statements hold.*

(a) If $(u(t), v(t))$ is a coexistence state, then $(\overline{u}_p, \overline{v}_p) \in C_p$. In particular, $C_p \neq \emptyset$ for every $p \in [1,\infty]$.

(b) Suppose we have at least one coexistence state. If

$$T\left(\sqrt{c_M e_M x_p y_p} + \frac{1}{2}(b_M x_1 + f_M y_1)\right) \leqslant \frac{\mathcal{J}(q)}{2^{2-\frac{1}{q}}}$$

for every $(x_p, y_p) \in C_p$ and $(x_1, y_1) \in C_1$, then such coexistence state is unique and asymptotically stable.

Remark 2.2. As presented in the introduction, we recall that the existence of a coexistence state is completely characterized. Therefore, the hypothesis of having at least one is not a loss of generality.

It follows from Hölder's inequality that if $\varphi \geqslant 0$, then $\overline{\varphi}_{p_1} \leqslant \overline{\varphi}_{p_2}$ for $1 \leqslant p_1 \leqslant p_2 \leqslant \infty$. Hence, we can replace statement (b) of Theorem 2.1 for the following weak version.

(b') Suppose we have at least one coexistence state. If

$$T\left(\sqrt{c_M e_M x_p y_p} + \frac{1}{2}(b_M x_p + f_M y_p)\right) \leqslant \frac{\mathcal{J}(q)}{2^{2-\frac{1}{q}}}$$

for every $(x_p, y_p) \in C_p$, then such coexistence state is unique and asymptotically stable.

Remark 2.3 (The L_1-condition)**.** Observe that if we replace $p = 1$ at Theorem 2.1(b), we obtain

$$T\left(\sqrt{c_M e_M x y} + \frac{1}{2}(b_M x + f_M y)\right) \leqslant 2$$

for every $(x, y) \in C_1$, where $C_1 \subset \mathbb{R}^2$ is the set bounded by $x > 0$, $y > 0$ and

$$\begin{aligned} b_L x + c_L y \leqslant \quad \overline{a} \quad &\leqslant b_M x + c_M y \\ -e_M x + f_L y \leqslant \quad \overline{d} \quad &\leqslant -e_L x + f_M y. \end{aligned}$$

This is precisely the L_1-condition obtained by R. Ortega [5, Theorem 5.2].

Remark 2.4 (The L_∞-condition)**.** Observe that if we replace $p = \infty$, $x = U$ and $y = V$ at Theorem 2.1(b'), we obtain

$$T\left(\sqrt{c_M e_M U V} + \frac{1}{2}(b_M U + f_M V)\right) \leqslant \pi. \tag{2.2}$$

This is the L_∞-condition obtained by R. Ortega and Amine [1, Proposition 4.5].

3 Preliminary results

In this section we recall the L_p-*condition* obtained by V. Ortega and Rebelo [6, Theorem 3.1] and also a technical lemma.

Theorem 3.1 (The L_p-condition)**.** *Suppose that all possible coexistence states* (u, v) *of system* (1.1) *satisfy*[1]

$$T^{\frac{1}{q}}\sqrt{\|eu\|_p \|cv\|_p} + \frac{1}{2}\|bu - fv\|_1 \leqslant \frac{\mathcal{J}(q)}{2^{2-\frac{1}{q}}}, \tag{3.1}$$

where p *and* q *are conjugated indices and* $p, q \in [1, \infty]$*. Then the coexistence state is unique and asymptotically stable. Moreover, any coexistence state* (u, v) *satisfies*

$$\|u\|_p \leqslant \frac{\|a\|_p}{b_L}, \quad \|v\|_p \leqslant \frac{\|d\|_p}{f_L} + \frac{e_M}{f_L}\frac{\|a\|_p}{b_L}. \tag{3.2}$$

Lemma 3.2. *Let* $(u(t), v(t))$ *be a coexistence state of* (1.1)*. Then* $\|u\|_\infty \leqslant U$ *and* $\|v\|_\infty \leqslant V$.

Proof. Let $\tau \in [0, T]$ be such that $u(\tau) = \max_{[0,T]} u(t)$. Since $u(\tau)$ is a local maximum, it follows that $\dot{u}(\tau) = 0$ and thus it follows from the first equation of (1.1) that

$$a(\tau) = b(\tau)u(\tau) + c(\tau)v(\tau) \geqslant b(\tau)u(\tau) \Rightarrow u(\tau) \leqslant \frac{a(\tau)}{b(\tau)} \leqslant U.$$

Similarly, if we let $\tau \in [0, T]$ be such that $v(\tau) = \max_{[0,T]} v(t)$, then it follows from the second equation of (1.1) that,

$$f(\tau)v(\tau) = d(\tau) + e(\tau)u(\tau) \Rightarrow v(\tau) \leqslant \frac{d(\tau)}{f(\tau)} + \frac{e(\tau)}{f(\tau)}u(\tau) \leqslant V.$$

This finishes the proof. □

For lower bound of the coexistence states of (1.1), we refer to [4, Lemma 5.5].

[1] Actually in their paper instead of the fraction $1/2$ in the expression, it appears the fraction $T/2$. But from equation (7) in that paper one can see that it is a typo.

4 Proof of Theorem 2.1

Before we prove the theorem, we observe that given $p \in [1,\infty]$ and $\varphi \in L^P$, it follows from Hölder's inequality that,

$$\|\varphi\|_1 \leqslant T^{1-\frac{1}{p}}\|\varphi\|_p. \tag{4.1}$$

Moreover, it follows from Littlewood's inequality that

$$\|\varphi\|_p \leqslant \|\varphi\|_1^{\frac{1}{p}}\|\varphi\|_\infty^{1-\frac{1}{p}},$$

and thus

$$\|\varphi\|_1 \geqslant \frac{1}{\|\varphi\|_\infty^{p-1}}\|\varphi\|_p^p. \tag{4.2}$$

Proof of Theorem 2.1. Let $(u(t),v(t))$ be a coexistence state of (1.1). Dividing the first equation of (1.1) by u we obtain,

$$\frac{\dot{u}}{u} = a(t) - b(t)u - c(t)v. \tag{4.3}$$

Integrating (4.3) in t, from 0 to T, we obtain

$$\int_0^T a = \int_0^T bu + \int_0^T cv,$$

and thus,

$$b_L\int_0^T u + c_L\int_0^T v \leqslant \int_0^T a \leqslant b_M\int_0^T u + c_M\int_0^T v. \tag{4.4}$$

Since $u \geqslant 0$ and $v \geqslant 0$, it follows from (4.4) that,

$$b_L\|u\|_1 + c_L\|v\|_1 \leqslant \int_0^T a \leqslant b_M\|u\|_1 + c_M\|v\|_1. \tag{4.5}$$

Applying (4.1) on the right-hand side of (4.5) we obtain

$$\int_0^T a \leqslant b_M T^{1-\frac{1}{p}}\|u\|_p + c_M T^{1-\frac{1}{p}}\|v\|_p. \tag{4.6}$$

Dividing (4.6) by T and knowing that $T^{-\frac{1}{p}}\|u\|_p = \overline{u}_p$ and $T^{-\frac{1}{p}}\|v\|_p = \overline{v}_p$ we obtain,

$$\overline{a} \leqslant b_M\overline{u}_p + c_M\overline{v}_p. \tag{4.7}$$

Similarly, applying (4.2) on the left-hand side of (4.5) we obtain,

$$\int_0^T a \geqslant b_L\frac{1}{\|u\|_\infty^{p-1}}\|u\|_p^p + c_L\frac{1}{\|v\|_\infty^{p-1}}\|v\|_p^p.$$

Hence, it follows from Lemma 3.2 that,

$$\int_0^T a \geqslant b_L\frac{1}{U^{p-1}}\|u\|_p^p + c_L\frac{1}{V^{p-1}}\|v\|_p^p. \tag{4.8}$$

Multiplying (4.8) by T^{-1} we obtain,

$$\overline{a} \geqslant b_L\frac{1}{U^{p-1}}\overline{u}_p^p + c_L\frac{1}{V^{p-1}}\overline{v}_p^p. \tag{4.9}$$

Let us now look to the second equation of (1.1). Dividing it by v and integrating it in t, from 0 to T, we obtain

$$\int_0^T d = -\int_0^T eu + \int_0^T fv,$$

and thus,

$$-e_M\|u\|_1 + f_L\|v\|_1 \leqslant \int_0^T d \leqslant -e_L\|u\|_1 + f_M\|v\|_1. \tag{4.10}$$

Applying (4.1) (resp. (4.2) and Lemma 3.2) on the positive (resp. negative) term of the right-hand side of (4.10) we obtain,

$$\int_0^T d \leqslant -e_L\frac{1}{U^{p-1}}\|u\|_p^p + f_M T^{1-\frac{1}{p}}\|v\|_p. \tag{4.11}$$

Multiplying (4.11) by T^{-1} we obtain,

$$\overline{d} \leqslant -e_L\frac{1}{U^{p-1}}\overline{u}_p^p + f_M\overline{v}_p. \tag{4.12}$$

Similarly, it follows from the left-hand side of (4.10) that,

$$\overline{d} \geqslant -e_M\overline{u}_p + f_L\frac{1}{V^{p-1}}\overline{v}_p^p. \tag{4.13}$$

Now observe that equations (4.7), (4.9), (4.12) and (4.13) are the four equations given at the definition (2.1) of the set C_p. Hence, we obtained statement (a) of Theorem 2.1.

Statement (b) follows directly from Theorem 3.1. More precisely, knowing that

$$\|eu\|_p \leqslant e_M\|u\|_p, \quad \|cv\|_p \leqslant c_M\|v\|_p, \quad \|bu - fv\|_1 \leqslant b_M\|u\|_1 + f_M\|v\|_1,$$

$\|u\|_1 = T\overline{u}_1$, $\|v\|_1 = T\overline{v}_1$, and $T^{\frac{1}{q}} = T/T^{\frac{1}{p}}$, one can see that the left-hand side of (3.1) can be majored by,

$$T\left(\sqrt{c_M e_M \overline{u}_p \overline{v}_p} + \frac{1}{2}(b_M\overline{u}_1 + f_M\overline{v}_1)\right).$$

Since every possible coexistence state (u,v) satisfies $(\overline{u}_p, \overline{v}_p) \in C_p$, we have from Theorem 3.1 that if

$$T\left(\sqrt{c_M e_M x_p y_p} + \frac{1}{2}(b_M x_1 + f_M y_1)\right) \leqslant \frac{\mathcal{J}(q)}{2^{2-\frac{1}{q}}}$$

for every $(x_p, y_p) \in C_p$ and $(x_1, y_1) \in C_1$, then the coexistence state is unique and asymptotically stable. □

5 An example and further thoughts

At first glance, one could look at the proof of Theorem 2.1 and conclude that since the boundaries of C_p are obtained by majoration and minoration of the boundaries of C_1 (which in turn was obtained by R. Ortega [5, p. 11]), then no new information could be drawn from such theorem. However, as the next example will show, this is not the case.

Example 5.1. Consider a Lotka–Volterra system

$$\dot{u} = u(a - bu - cv), \quad \dot{v} = v(d + eu - fv), \tag{5.1}$$

with the coefficients being positive constant. We recall the sufficient condition

$$T\left(\sqrt{c_M e_M x_p y_p}+\frac{1}{2}(b_M x_1+f_M y_1)\right)\leqslant\frac{\mathcal{J}(q)}{2^{2-\frac{1}{q}}} \tag{5.2}$$

of Theorem 2.1(b). Let $F(q)=\mathcal{J}(q)/2^{2-\frac{1}{q}}$, where $q=p/(p-1)$ is the conjugate of p, and let also $\mathcal{F}(p)=F(p/(p-1))$ (see Appendix C). Since the coefficients of (5.1) are constant, it is not hard to see that $C_1=\{(x_1,y_1)\}$ is a single point, given by the unique solution of

$$\begin{pmatrix} b & c\\ -e & f\end{pmatrix}\begin{pmatrix} x_1\\ y_1\end{pmatrix}=\begin{pmatrix} a\\ d\end{pmatrix}.$$

Let $k=(b_M x_1+f_M y_1)/2$ and observe that we can write (5.2) as $x_p^p y_p^p\leqslant h(p)$, where

$$h(p)=\left[\frac{1}{\sqrt{ce}}\left(\frac{\mathcal{F}(p)}{T}-k\right)\right]^{2p}.$$

We recall that $C_p\subset\mathbb{R}^2$ is the set bounded by $x>0$, $y>0$ and

$$\begin{aligned} b_L U^{1-p}x^p+c_L V^{1-p}y^p\leqslant\overline{a}\leqslant b_M x+c_M y\\ -e_M x+f_L V^{1-p}y^p\leqslant\overline{d}\leqslant -e_L U^{1-p}x^p+f_M y,\end{aligned} \tag{5.3}$$

if $p\in[1,\infty)$, and by

$$0<x\leqslant U,\quad 0<y\leqslant V,$$

if $p=\infty$ (for an illustration, see Appendix B). Therefore, since the left-hand side of (5.2) is an increasing function of x_p and y_p (recall that x_1 and y_1 are constant), we have from (5.3) that its maximum happens somewhere on the curve

$$bU^{1-p}x_p^p+cV^{1-p}y_p^p=a.$$

Hence, the maximum occurs at some point (x_p,y_p) such that

$$y_p^p=c^{-1}V^{p-1}(a-bU^{1-p}x_p^p). \tag{5.4}$$

Replacing (5.4) at $x_p^p y_p^p\leqslant h(p)$, we obtain

$$-\left[\frac{b}{c}\left(\frac{V}{U}\right)^{p-1}\right]w^2+\left[\frac{a}{c}V^{p-1}\right]w-h(p)\leqslant 0, \tag{5.5}$$

where $w=x_p^p$. The discriminant of (5.5) in relation to w is given by,

$$\Delta(p)=V^{p-1}\left[\frac{a^2}{c^2}V^{p-1}-4\frac{b}{c}\frac{1}{U^{p-1}}h(p)\right].$$

Therefore, to study its sign it is sufficient to study the sign of

$$G(p)=\frac{a^2}{c^2}V^{p-1}-4\frac{b}{c}\frac{1}{U^{p-1}}h(p).$$

From this reasoning we have that (5.2) is equivalent to (5.5). Since the leading coefficient of the left-hand side of (5.5) is negative, it follows that the inequality holds at a given $p\in[1,\infty)$ if, and only if, $G(p)\leqslant 0$.

Hence, we conclude that we can apply Theorem 2.1 at (5.1) at a given $p \in [1,\infty)$ if, and only if, $G(p) \leqslant 0$. Therefore, if for some choice of the coefficients we have

$$G(1) > 0, \quad G(p^*) < 0, \quad \lim_{p\to\infty} G(p) > 0, \tag{5.6}$$

for some $p^* \in (1,\infty)$, then the L_1 and L_∞-conditions (recall Remarks 2.3 and 2.4) will be inconclusive. Moreover, since the coefficients are constant we have

$$\frac{\|a\|_p}{b_L} = U, \quad \frac{\|d\|_p}{f_L} + \frac{e_M}{f_L}\frac{\|a\|_p}{b_L} = V,$$

and thus the upper bound (3.2) is reduced to $\overline{u}_p \leqslant U$ and $\overline{v}_p \leqslant V$. As a consequence, it follows that when applying the L_p-condition in the way it was stated at Theorem 3.1, the only known upper bounds for $\|u\|_p$ and $\|v\|_p$, $p \in [1,\infty]$, are given by U and V, respectively. Therefore, equation (3.1) is reduced to

$$T\left(\sqrt{c_M e_M UV} + \frac{1}{2}(b_M U + f_M V)\right) \leqslant \frac{\mathcal{J}(q)}{2^{2-\frac{1}{q}}} \leqslant \pi, \tag{5.7}$$

with the last inequality following from Proposition C.1 (see also Figure C.1). Since the L_∞-condition is inconclusive, it follows that (2.2) does not hold and thus (5.7) also does not hold.

Therefore we conclude that if (5.6) holds, then the L_1 and L_∞-conditions are inconclusive, while the upper bounds (3.2) provided by the L_p-condition, in the way it was stated at Theorem 3.1, are too thick and also inconclusive. Nevertheless, Theorem 2.1 can still be applied at $p = p^*$, ensuring the uniqueness and asymptotically stability of the coexistence state.

In other words, Theorem 3.1 still holds, since it state that (3.1) must hold for all the *coexistence states* of the system. However, the practical upper bounds provided by (3.2) are too thick in the case of this example, while the upper bounds provided by Theorem 2.1 are not.

For an example of such situation, one can consider $T = 1$,

$$a = 2.0102, \quad b = 1, \quad c = 0.0051, \quad d = 2.0203, \quad e = 0.9898, \quad f = 2, \tag{5.8}$$

and see that (5.6) holds with $p^* = 2$.

Remark 5.2. We have assumed constant coefficients at Example 5.1 for the sake of simplicity. However, it follows from the continuous dependence of the boundaries of C_p, $p \in [1,\infty]$, in relation to the coefficient functions $a(t),\dots,f(t)$ that if the amplitude of such coefficients (i.e. $a_M - a_L,\dots,f_M - a_L$) is small enough and if their averages are close enough to (5.8), then the same conclusion holds. Moreover, the assumption $T = 1$ is no loss of generality since it can be obtained by time rescaling.

We think that one reason for Theorem 2.1 to be conclusive in some situations while the previous one are not is the fact that although the boundaries of C_p are obtained by inequalities on the boundaries of C_1, the function $\mathcal{F}(p)$ *also increases* (see Appendix C). Therefore, for a given $p \in (1,\infty)$, the function $\mathcal{F}(p)$ may have increased in such a way that it compensates the boundaries of C_p.

Moreover in comparison with the boundaries provided by (3.2), as anticipated in the introduction, the fact that the two inequalities are independent from each other provides a *unified* test for uniqueness and asymptotically stability of the coexistence states. More precisely, if

$$T^{\frac{1}{q}}\sqrt{c_M e_M \alpha_p \beta_p} + \frac{1}{2}(b_M\alpha_1 + f_M\beta_1) \leqslant \frac{\mathcal{J}(q)}{2^{2-\frac{1}{q}}}$$

for some $p \in [1, \infty]$, where

$$\alpha_p = \frac{\|a\|_p}{b_L}, \quad \beta_p = \frac{\|d\|_p}{f_L} + \frac{e_M}{f_L}\frac{\|a\|_p}{b_L},$$

then we are done. However, if the unified test is inconclusive then the intertwined boundaries (2.1) of C_p can reduce the lack of possibilities of the averages of the coexistence states in such a way that for all *possible* coexistence states, inequality (3.1) still holds.

A Linearly stability, asymptotic stability and Floquet theory

Consider a system T-periodic system of differential equations

$$\dot{u} = H(t, u), \tag{A.1}$$

with $u \in \mathbb{R}^n$ and $H\colon \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}^n$ sufficiently smooth. Let $u_0(t)$ be a T-periodic solution of (A.1). The *linearization* of (A.1) at $u_0(t)$ is the T-periodic linear system given by

$$\dot{u} = D_u H(t, u_0(t))u, \tag{A.2}$$

where $D_u H$ denotes the Jacobian matrix of H with respect to the variable u. We say that $u_0(t)$ is *linearly stable* if all *Floquet exponents* (also known as *characteristics exponents*) associated to (A.2) have non-positive real part. Fore more details about Floquet Theory, we refer to [3, Section 3.5] and [7].

We say that u_0 is *stable* if for every neighborhood $V \subset \mathbb{R}^n$ of $u_0(0)$ there is a neighborhood $W \subset V$ of $u_0(0)$ such that if $u(t)$ is a solution of (A.1) with $u(0) \in W$, then $u(t) \in V$ for $t \geqslant 0$. Moreover, given an open set $U \subset \mathbb{R}^n$, we say that $u_0(t)$ is *asymptotically stable* in U if u_0 is stable and

$$\lim_{t \to \infty} |u_0(t) - u(t)| = 0,$$

for every solution $u(t)$ of (A.1) with $u(0) \in U$.

B Illustrations of the set C_p and construction of C_∞

We recall that $C_p \subset \mathbb{R}^2$ is the set bounded by $x > 0$, $y > 0$ and

$$\begin{aligned} b_L U^{1-p} x^p + c_L V^{1-p} y^p &\leqslant \overline{a} \leqslant b_M x + c_M y \\ -e_M x + f_L V^{1-p} y^p &\leqslant \overline{d} \leqslant -e_L U^{1-p} x^p + f_M y, \end{aligned}$$

for $p \in [1, \infty)$, and by

$$0 < x \leqslant U, \quad 0 < y \leqslant V,$$

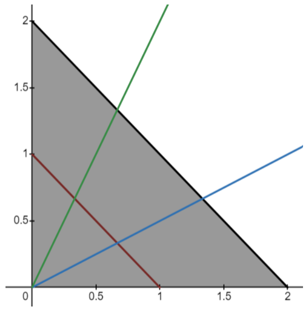
for $p = \infty$. See Figure B.1. To obtain the definition of C^∞, consider the inequality

$$b_L U^{1-p} x^p + c_L V^{1-p} y^p \leqslant \overline{a}. \tag{B.1}$$

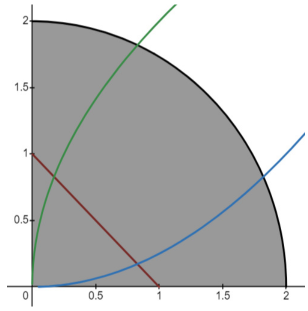
Since the left-hand side is strictly increasing in x and y it is clear that the maximum value of x occurs when $y = 0$. Hence, replacing $y = 0$ at (B.1) we obtain,

$$x \leqslant \left(\frac{\overline{a}}{b_L}\right)^{\frac{1}{p}} U^{\frac{1}{q}}.$$

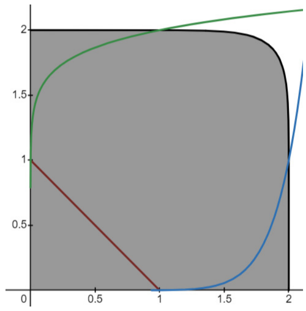
Taking the limit $p \to \infty$ we obtain $x \leqslant U$. Similarly, by replacing $x = 0$ at (B.1) and taking the limit $p \to \infty$ one obtains $y \leqslant V$.



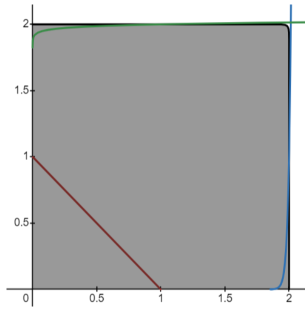
$p = 1.$



$p = 2.$



$p = 10.$



$p = 100.$

Figure B.1: Illustrations of C_p, given by the region bounded by the four curves, with parameters $\overline{a} = 2$, $\overline{d} = 2$, $b_M = 2$, $b_L = 1$, $c_M = 2$, $c_L = 1$, $e_M = 2$, $e_L = 1$, $f_M = 2$, $f_L = 1$, $U = 2$ and $V = 2$. The gray region (resp. black curve) corresponds to the inequality (resp. equality) $b_L U^{1-p} x^p + c_L V^{1-p} y^p \leqslant \overline{a}$. The red curve correspond to $b_M x + c_M y = \overline{a}$, while the green the blue ones correspond to $-e_M x + f_L V^{1-p} y^p = \overline{d}$ and $-e_L U^{1-p} x^p + f_M y = \overline{d}$, respectively. Together, they form the boundaries of C_p. Colors available in the online version.

C Properties of the maps $\mathcal{J}$, F and $\mathcal{F}$

We recall that $\mathcal{J}\colon [1,\infty) \to \mathbb{R}$ is the function given by,

$$\mathcal{J}(q) = \int_0^{2\pi} \frac{1}{\left(|\cos\theta|^{2q} + |\sin\theta|^{2q}\right)^{\frac{1}{q}}}\, d\theta. \tag{C.1}$$

Moreover, it follows from [6, Proposition 2.2] that

$$\lim_{q\to\infty} \mathcal{J}(q) = 8,$$

and thus we can continuously extend $\mathcal{J}$ to $[1,\infty]$ by defining $\mathcal{J}(\infty) = 8$. We also recall that $F, \mathcal{F}\colon [1,\infty] \to \mathbb{R}$ are the functions given by

$$F(q) = \frac{\mathcal{J}(q)}{2^{2-\frac{1}{q}}}, \quad \mathcal{F}(p) = F\left(\frac{p}{p-1}\right) = \frac{\mathcal{J}\left(\frac{p}{p-1}\right)}{2^{1+\frac{1}{p}}}, \tag{C.2}$$

where $q = p/(p-1)$ is the conjugate of p. For a numerical plot of the graph of $\mathcal{F}(p)$, see Figure C.1.

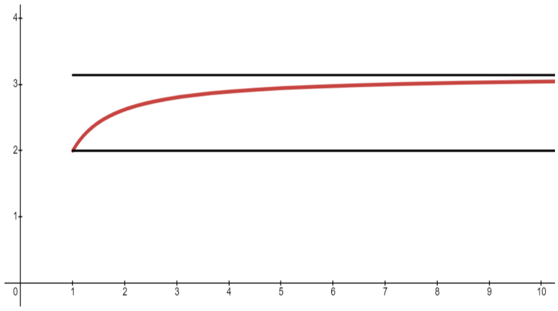


Figure C.1: Graph of the function $\mathcal{F}(p)$, in red. The black straight lines are the lower and upper bounds $y = 2$ and $y = \pi$, respectively. Colors available in the online version.

Proposition C.1. *The functions F and $\mathcal{F}$ are strictly decreasing and increasing, respectively.*

Proof. First we consider the function F. That is, we consider

$$F(q) = \frac{\mathcal{J}(q)}{2^{2-\frac{1}{q}}} = \int_0^{2\pi} 2^{\frac{1}{q}-2}\big(|\cos\theta|^{2q} + |\sin\theta|^{2q}\big)^{-\frac{1}{q}}\,d\theta. \tag{C.3}$$

Consider the integrand of the outermost right-hand side of (C.3),

$$g_1(\theta,q) = 2^{\frac{1}{q}-2}\big(|\cos\theta|^{2q} + |\sin\theta|^{2q}\big)^{-\frac{1}{q}}.$$

Differentiating it in relation to q we obtain

$$\frac{\partial g_1}{\partial q}(\theta,q) = g_1(\theta,q)\left[\frac{1}{q^2(\cos^{2q}\theta + \sin^{2q}\theta)}g_2(\theta,q) + \ln\big(2^{-1/q^2}\big)\right], \tag{C.4}$$

where

$$\begin{aligned} g_2(\theta,q) = \ & \cos^{2q}\theta\big[\ln(\cos^{2q}\theta + \sin^{2q}\theta) - \ln\cos^{2q}\theta\big] \\ & + \sin^{2q}\theta\big[\ln(\cos^{2q}\theta + \sin^{2q}\theta) - \ln\sin^{2q}\theta\big]. \end{aligned} \tag{C.5}$$

Since g_1 is strictly positive, it follows that the sign of (C.4) is given by the sign of,

$$\frac{1}{q^2(\cos^{2q}\theta + \sin^{2q}\theta)}g_2(\theta,q) + \ln\big(2^{-1/q^2}\big). \tag{C.6}$$

We claim that (C.6) is negative. Indeed, observe that (C.6) is negative if and only if,

$$g_2(\theta,q) \leqslant -q^2(\cos^{2q}\theta + \sin^{2q}\theta)\ln\big(2^{-1/q^2}\big).$$

Which by properties of the logarithm is equivalent to,

$$g_2(\theta,q) \leqslant (\cos^{2q}\theta + \sin^{2q}\theta)\ln 2.$$

Which in turn is equivalent to,

$$\begin{aligned} g_3(\theta,q) := \ & \cos^{2q}\big[\ln(\cos^{2q}\theta + \sin^{2q}\theta) - \ln(2\cos^{2q}\theta)\big] \\ & + \sin^{2q}\big[\ln(\cos^{2q}\theta + \sin^{2q}\theta) - \ln(2\sin^{2q}\theta)\big] \leqslant 0. \end{aligned} \tag{C.7}$$

Differentiating (C.7) in relation to θ we obtain,

$$\frac{\partial g_3}{\partial \theta}(\theta,q) = 2q\sin\theta\cos\theta\Big[\cos^{2(q-1)}\theta\big[\ln(2\cos^{2q}\theta)-\ln(\cos^{2q}\theta+\sin^{2q}\theta)\big] \\ -\sin^{2(q-1)}\theta\big[\ln(2\sin^{2q}\theta)-\ln(\cos^{2q}\theta+\sin^{2q}\theta)\big]\Big]. \quad \text{(C.8)}$$

Clearly, the zeros of (C.8) in θ are given by $\theta \in \{0, \pi/2, \pi, 3\pi/2\}$ and by the zeros of

$$g_4(\theta,q) := \cos^{2(q-1)}\theta\big[\ln(2\cos^{2q}\theta)-\ln(\cos^{2q}\theta+\sin^{2q}\theta)\big] \\ -\sin^{2(q-1)}\theta\big[\ln(2\sin^{2q}\theta)-\ln(\cos^{2q}\theta+\sin^{2q}\theta)\big]. \quad \text{(C.9)}$$

Observe that if $\theta_0 \in [0,2\pi]$ is such that $\cos^2\theta_0 = \sin^2\theta_0$, then $g_4(\theta_0,q) = 0$. Reciprocally, we claim that if $\cos^2\theta_0 \neq 0\sin^2\theta_0$, then $g_4(\theta_0,q) \neq 0$. Indeed, if $\cos^2\theta_0 > \sin^2\theta_0$, then it follows from the fact that the logarithm is a strictly increasing function that,

$$\ln(2\cos^{2q}\theta_0) > \ln(\cos^{2q}\theta_0+\sin^{2q}\theta_0), \quad \ln(2\sin^{2q}\theta_0) < \ln(\cos^{2q}\theta_0+\sin^{2q}\theta_0).$$

Hence, $g_4(\theta_0,q) > 0$. Similarly if $\cos^2\theta_0 < \sin^2\theta_0$, then $g_4(\theta_0,q) < 0$.

Therefore, we conclude that the extreme points $\theta_0 \in [0,2\pi]$ of (C.7) are such that $\cos\theta_0\sin\theta_0 = 0$ or $\cos^2\theta_0 = \sin^2\theta_0$. In any case, it is easy to see that (C.7) holds (with the equality holding only if $\cos^2\theta_0 = \sin^2\theta_0$), which in turn implies that the same holds for (C.4). Therefore, it follows from Leibniz integral rule that

$$F'(q) = \int_0^{2\pi} \frac{\partial g_1}{\partial q}(\theta,q)\,d\theta < 0.$$

That is, $F'(q)$ is strictly decreasing. Since $\mathcal{F}(p) = F(p/(p-1))$, it follows that

$$\mathcal{F}'(p) = -\frac{1}{(p-1)^2}F'\left(\frac{p}{p-1}\right) > 0,$$

and thus $\mathcal{F}$ is strictly increasing. □

Remark C.2. With the same reasoning of Proposition C.1, one can prove that $\mathcal{J}(q)$ is also strictly increasing. One just need to consider the integrand

$$h_1(\theta,q) = \frac{1}{(|\cos\theta|^{2q}+|\sin\theta|^{2q})^{\frac{1}{q}}},$$

observe that

$$\frac{\partial h_1}{\partial q}(\theta,q) = \frac{h_1(\theta,q)}{q^2(\cos^{2q}\theta+\sin^{2q}\theta)}g_2(\theta,q),$$

with g_2 given by (C.5), and observe that since the logarithm is strictly increasing, it follows that

$$\ln(\cos^{2q}\theta+\sin^{2q}\theta) \geqslant \ln\cos^{2q}\theta, \quad \ln(\cos^{2q}\theta+\sin^{2q}\theta) \geqslant \ln\sin^{2q}\theta,$$

with equality holding only if $\cos\theta\sin\theta = 0$. The proof now follows from Leibniz integral rule.

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