Applied Mathematics and Computation 226 (2014) 754–764

Contents lists available at ScienceDirect

Applied Mathematics and Computation

journal homepage: www.elsevier.com/locate/amc

Lyapunov functionals for two-species mutualisms

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ARTICLE INFO

Keywords:
Mutualistic interaction
Global stability
Lyapunov functional
Monotonicity properties

ABSTRACT

We analyze the dynamics of a general model of two-species mutualistic interaction given in an abstract, unspecified form, which fits several commonly used concrete models. Sufficient conditions for the global stability of the positive equilibrium are obtained by means of employing Lyapunov's second method, for functionals which are defined *ad hoc* and are strictly more general than both quadratic and Volterra functionals. It is observed that the complexity of such conditions increases drastically when key monotonicity properties are weakened.

1. Introduction

A mutualistic association between two or more species represents a relationship in which all of them experience a positive effect from their interaction, consisting in an increase of their ability to survive, grow or reproduce. Mutualistic symbioses such as those between the cells of ancient eukaryotic organisms and formerly independent microorganisms such as mitochondria or plasmids made possible the very existence of current living organisms (Margulis [17]), and certain such mutualistic symbioses remain among the most important ecological interactions on this planet even today. Most terrestrial plants rely on mycorrizhae for the uptake of phosphate or of other mineral nutrients, and on various pollination and seed dispersal mutualisms for their reproduction.

Also, the following findings have been reported in Bäckhed et al. [2]):"New studies are revealing how the gut microbiota has coevolved with us and how it manipulates and complements our biology in ways that are mutually beneficial. Bacteroides thetaiotaomicron is a prominent mutualist in the distal intestinal habitat of adult humans. [...] The guts of ruminants and termites are well-studied examples of bioreactors "programmed" with anaerobic bacteria charged with the task of breaking down ingested polysaccharides, the most abundant biological polymer on our planet, and fermenting the resulting monosaccharide soup to short-chain fatty acids. In these mutualistic relationships, the hosts gain carbon and energy, and their microbes are provided with a rich buffet of glycans and a protected anoxic environment."

It can be argued that mutualism drives evolution and, in a functional organism, trophic chain, or even social system, mutualisms occur at multiple spatial or temporal scales.

By degree of dependency, mutualisms can be classified into facultative and obligate. Facultative mutualists can survive independently, while obligate mutualists can survive only in association to each other, being biologically incapable of surviving without their partner (Pastor [20]). It has been predicted by Bronstein in [3] that the outcomes of facultative mutualisms should be more variable than the outcome of more obligate mutualisms. Certain facultative mutualisms derived from Lotka-Volterra model involve a positive feedback which is potentially destabilizing (May [18]), although this does not match

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http://dx.doi.org/10.1016/j.amc.2013.10.061

real-world evidence (Lewis [12], Heithaus et al. [9]). It has been consequently observed by Addicott [1] that the structural instability of the models of mutualism is actually a function of a biologically inappropriate assumption.

Moreover, it has been argued in Ringel et al. [21] that mutualisms have actually a stabilizing effect when they are embedded in realistic multispecies real-world communities, such as the four-species model of a pollination mutualism proposed in [21] and it has been observed by Addicott [1] that the consideration of most kinds of mutualism and most kinds of stability criteria shows that a mutualism is more stable than the corresponding system without mutualism. Also, Goh [5] has proved that in a two species Lotka-Volterra model of mutualism local stability implies global stability.

Mutualisms have much in common with predator–prey or parasitic relationships, from which many of them are thought to have evolved. In such mutualisms, the negatively affected organism has adapted to the initially disadvantageous relationship, a truly mutually beneficial association evolving as a consequence. However, mutualisms have historically received far less attention than other interactions such as predation and parasitism, although recent studies call for an integration of several interaction types in complex food webs, being found that high mutualistic to antagonistic ratios generate significantly more diversity than found in the randomized networks (Melián et al. [19]).

In Vargas-De-León [23], paper which motivated our work, global stability conditions for two species models of mutualism are obtained by means of using suitably constructed Lyapunov functionals and LaSalle's invariance principle. The models discussed therein are

$$\begin{aligned} \frac{dx_1}{dt} &= r_1x_1\left[\left(1-\frac{e_1}{r_1}\right)-\frac{x_1}{K_1}\right]+\frac{r_1b_{12}}{K_1}x_1x_2 \\ \frac{dx_2}{dt} &= r_2x_2\left[\left(1-\frac{e_2}{r_2}\right)-\frac{x_2}{K_2}\right]+\frac{r_2b_{21}}{K_2}x_1x_2, \end{aligned} \tag{1}$$

introduced by Vandermeer and Boucher in [22] to account for the situation in which the effects of mutualism are density independent (see also the corresponding discussion in Wolin and Lawlor [25]), and

$$\begin{aligned} \frac{dx_1}{dt} &= (r_1-e_1)x_1-\frac{r_1x_1^2}{K_1+b_{12}x_2} \\ \frac{dx_2}{dt} &= (r_2-e_2)x_2-\frac{r_2x_2^2}{K_2+b_{21}x_1}, \end{aligned} \tag{2}$$

introduced by Wolin and Lawlor in [25] to account for the situation in which mutualism has the most impact when the recipient population is at high density (see also Kot [16], p. 233). In the above models, r_i is the intrinsic birth rate of species x_i, while K_i and e_i represent the carrying capacity of the environment and the harvesting effort, respectively, with regard to the same species $x_i, i=1,2$. Also, b_{12} and b_{21} are strictly positive constants measuring the effects of interspecies cooperation on species x_1 and x_2, respectively, that is, the mutualistic support the species give each other. Both models above were initially introduced without accounting for the effect of harvesting. It is to be noted that both (1) and (2) are models of facultative mutualisms and if one species is missing then the equation which describes the dynamics of the other species is the same for both models and characterizes their logistic growth.

Let us denote $A_1 = 1-e_1/r_1, A_2 = 1-e_2/r_2$. Using the Lyapunov functionals

$$L_1(x_1,x_2) = c_1\int_{x_1^*}^{x_1}\frac{\theta-x_1^*}{(K_2+b_{21}\theta)\theta^2}d\theta + c_1\frac{r_1A_1b_{12}x_2^*}{r_2A_2b_{21}x_1^*}\int_{x_2^*}^{x_2}\frac{\theta-x_2^*}{(K_1+b_{12}\theta)\theta^2}d\theta$$

and

$$L_2(x_1,x_2) = c_1\left(\ln\frac{x_1}{x_1^*}+\frac{x_1^*}{x_1}-1\right)+c_1\frac{r_1b_{12}K_2x_2^*}{r_2b_{21}K_1x_1^*}\left(\ln\frac{x_2}{x_2^*}+\frac{x_2^*}{x_2}-1\right),$$

where $c_1 \in \mathbb{R}_+$ is arbitrary, Vargas-De-León established in [23] the following global stability results.

Theorem 1.1. *If*

$$b_{12}b_{21} < 1, \quad 0 \leqslant e_1 \leqslant r_1 \quad \text{and} \quad 0 \leqslant e_2 < r_2 \tag{3}$$

or

$$b_{12}b_{21} < 1, \quad 0 \leqslant e_1 < r_1 \quad \text{and} \quad 0 \leqslant e_2 \leqslant r_2, \tag{4}$$

then the system (1) *admits a unique coexisting equilibrium* (x_1^*, x_2^*) *in* $\mathrm{int}(\mathbb{R}_+^2)$, *with coordinates given by*

$$x_1^* = \frac{A_1K_1+b_{12}A_2K_2}{1-b_{12}b_{21}}, \quad x_2^* = \frac{A_2K_2+b_{21}A_1K_1}{1-b_{12}b_{21}},$$

which is globally asymptotically stable in $\mathrm{int}(\mathbb{R}_+^2)$.

Theorem 1.2. *If*

$$A_1A_2b_{12}b_{21} < 1, \quad 0 \leqslant e_1 < r_1 \quad \text{and} \quad 0 \leqslant e_2 < r_2, \tag{5}$$

then the system (2) admits a unique coexisting equilibrium (x_1^*, x_2^*) *in* $int(\mathbb{R}_+^2)$, *with coordinates given by*

$$x_1^* = \frac{A_1(K_1 + b_{12}A_2K_2)}{1 - A_1A_2b_{12}b_{21}}, \quad x_2^* = \frac{A_2(K_2 + b_{21}A_1K_1)}{1 - A_1A_2b_{12}b_{21}},$$

which is globally asymptotically stable in $\mathrm{int}(\mathbb{R}_+^2)$.

Furthermore, it has been observed that another set of Lyapunov functionals, namely

$$\widetilde{L_1}(x_1, x_2) = c_1 \int_{x_1^*}^{x_1} \frac{\theta - x_1^*}{(K_2 + b_{21}\theta)\theta} d\theta + c_1 \frac{r_1A_1b_{12}}{r_2A_2b_{21}} \int_{x_2^*}^{x_2} \frac{\theta - x_2^*}{(K_1 + b_{12}\theta)\theta} d\theta \tag{6}$$

and

$$\widetilde{L_2}(x_1, x_2) = c_1x_1^*\left(\frac{x_1}{x_1^*} - 1 - \ln\frac{x_1}{x_1^*}\right) + c_1\frac{r_1b_{12}K_2}{r_2b_{21}K_1}x_2^*\left(\frac{x_2}{x_2^*} - 1 - \ln\frac{x_2}{x_2^*}\right), \tag{7}$$

can be used as well to establish the conclusions of Theorems 1.1 and 1.2, the latter under the additional set of constraints

$$A_1b_{12} < 1, \quad A_2b_{21} < 1. \tag{8}$$

In what follows, we shall review the results of Vargas-De-León [23] in a more general context and, to this purpose, employ Lyapunov functionals which are applicable to a large class of two species cooperative models. See also Vargas-De-León and Gómez-Alcaraz [24] for a related investigation of a two species model of commensalism.

2. The model

Let us consider the model

$$\begin{aligned} \frac{dx_1}{dt} &= a_1(x_1) + f_1(x_1)g_1(x_2) \\ \frac{dx_2}{dt} &= a_2(x_2) + f_2(x_2)g_2(x_1), \end{aligned} \tag{9}$$

where $a_1, a_2, f_1, f_2, g_1, g_2$ are real continuous functions defined at least on $[0, \infty)$ which satisfy the following conditions.

(H1) The functions f_1, f_2 are strictly positive on $(0, \infty)$. The functions g_1, g_2 are nonzero on $(0, \infty)$.
(H2) The functions g_1 and g_2 are strictly increasing on $(0, \infty)$.

Hypotheses **(H1)** and **(H2)** imply together the fact that the abstract model (9) describes indeed a mutualism, in the sense that increasing the density of one population has a benefic effect on the growth of the other one. Of course, to represent concrete models, f_1, f_2, g_1, g_2 are not uniquely determined, but determined only up to a multiplicative constant and consequently f_1, f_2 can easily be chosen with positive sign. Note that the interaction terms $f_1(x_1)g_1(x_2)$ and $f_2(x_2)g_2(x_1)$ need not be positive (this is the case with the model (2), for instance), such negative interaction terms being used to represent the fact that the mutualistic association decreases the death rates of the respective species. In our settings, the interaction terms do not change sign, a sign change representing a transition between a mutualistic interaction and an association which is detrimental to one of the species. See Hernandez [10] for further details on this matter.

Also, since our focus is on discussing the stability of the positive equilibrium rather than establishing its existence, we shall assume the following existence condition.

(E) There is a unique coexisting equilibrium $\mathbf{E}^* = (x_1^*, x_2^*)$ of (9).

As a result, it is seen that the coordinates of $\mathbf{E}^*$ satisfy the following equilibrium conditions

$$a_1(x_1^*) + f_1(x_1^*)g_1(x_2^*) = 0, \quad a_2(x_2^*) + f_2(x_2^*)g_2(x_1^*) = 0. \tag{10}$$

3. Global stability with monotonicity

We now attempt to establish the global stability of $\mathbf{E}^*$ under certain monotonicity assumptions. To this purpose, we now introduce the first set of auxiliary conditions, in the following form.

(H3) The functions $\frac{a_1}{f_1} + g_2$ and $\frac{a_2}{f_2} + g_1$ are decreasing, at least one of them being strictly decreasing.
(I1) $\int_{x_i^*}^{\xi} \frac{g_j(\theta) - g_j(x_i^*)}{f_i(\theta)} d\theta = +\infty$, for $\xi \in \{0, \infty\}$ and $(i, j) \in \{(1, 2), (2, 1)\}$.

We are now ready to state our first global stability result.

Theorem 3.1. *If* **(H1)**, **(H2)**, **(H3)**, **(I1)** *and* **(E)** *are satisfied, then* $\mathbf{E}^*$ *is globally asymptotically stable in* $\mathrm{int}(\mathbb{R}^2_+)$.

Proof. We shall employ the following Lyapunov functional

$$V_1(x_1,x_2)=\int_{x_1^*}^{x_1}\frac{g_2(\theta)-g_2(x_1^*)}{f_1(\theta)}d\theta+\int_{x_2^*}^{x_2}\frac{g_1(\theta)-g_1(x_2^*)}{f_2(\theta)}d\theta \tag{11}$$

First, it is seen that from **(H1)** and **(H2)** that V_1 increases whenever any of $|x_1-x_1^*|$ and $|x_2-x_2^*|$ increases and $V_1(x_1,x_2)\geqslant 0$ for all $x_1,x_2\geqslant 0$, while $V_1(x_1,x_2)=0$ if and only if $x_1=x_1^*$ and $x_2=x_2^*$. Also, by **(I1)**, $V_1(x_1,x_2)$ tends to $+\infty$ if either x_1 or x_2 tends to 0 or to $+\infty$. One then has

$$\begin{aligned}\dot V_1&=\frac{g_2(x_1)-g_2(x_1^*)}{f_1(x_1)}(a_1(x_1)+f_1(x_1)g_1(x_2))+\frac{g_1(x_2)-g_1(x_2^*)}{f_2(x_2)}(a_2(x_2)+f_2(x_2)g_2(x_1))\\&=(g_2(x_1)-g_2(x_1^*))\left(\frac{a_1(x_1)}{f_1(x_1)}+g_1(x_2)\right)+(g_1(x_2)-g_1(x_2^*))\left(\frac{a_2(x_2)}{f_2(x_2)}+g_2(x_1)\right).\end{aligned}$$

From the equilibrium conditions (10), it is seen that

$$-\frac{a_1(x_1^*)}{f_1(x_1^*)}=g_1(x_2^*),\quad -\frac{a_2(x_2^*)}{f_2(x_2^*)}=g_2(x_1^*).$$

Consequently,

$$\dot V_1=(g_2(x_1)-g_2(x_1^*))\left(\frac{a_1(x_1)}{f_1(x_1)}-\frac{a_1(x_1^*)}{f_1(x_1^*)}\right)+(g_1(x_2)-g_1(x_2^*))\left(\frac{a_2(x_2)}{f_2(x_2)}-\frac{a_2(x_2^*)}{f_2(x_2^*)}\right)+2(g_2(x_1)-g_2(x_1^*))(g_1(x_2)-g_1(x_2^*)).$$

Having in view that $2ab\leqslant a^2+b^2$ for all $a,b\in\mathbb{R}$, one obtains that

$$\dot V_1\leqslant(g_2(x_1)-g_2(x_1^*))\left(\frac{a_1(x_1)}{f_1(x_1)}+g_2(x_1)-\frac{a_1(x_1^*)}{f_1(x_1^*)}-g_2(x_1^*)\right)+(g_1(x_2)-g_1(x_2^*))\left(\frac{a_2(x_2)}{f_2(x_2)}+g_1(x_2)-\frac{a_2(x_2^*)}{f_2(x_2^*)}-g_1(x_2^*)\right).$$

Noting that $\dot V_1\leqslant 0$, by **(H2)** and **(H3)**, with equality if and only if either $x_1=x_1^*$ or $x_2=x_2^*$ and, in any case, $\mathbf{E}^*$ is the only invariant set in $M=\left\{(x_1,x_2);\dot V_1(x_1,x_2)=0\right\}$, it follows by LaSalle's invariance principle that $\mathbf{E}^*$ is globally asymptotically stable in $\mathrm{int}(\mathbb{R}^2_+)$.

To relate our result with those of [23], let us rearrange the model (1) in the form

$$\begin{aligned}\frac{dx_1}{dt}&=r_1x_1\left(A_1-\frac{x_1}{K_1}\right)+r_1\frac{b_{12}}{K_1}x_1x_2\\\frac{dx_2}{dt}&=r_2x_2\left(A_2-\frac{x_2}{K_2}\right)+r_2\frac{b_{21}}{K_2}x_1x_2,\end{aligned}\tag{12}$$

choose

$$a_1(x_1)=r_1x_1\left(A_1-\frac{x_1}{K_1}\right),\ a_2(x_2)=r_2x_2\left(A_2-\frac{x_2}{K_2}\right),\ f_1(x_1)=r_1\frac{b_{12}}{K_1}x_1,\ g_1(x_2)=x_2,\ f_2(x_2)=\frac{r_2x_2}{K_2},\ g_2(x_1)=b_{21}x_1,$$

and assume that either (3) or (4) are satisfied. In this case,

$$\frac{a_1}{f_1}(x_1)=\frac{K_1}{b_{12}}\left(A_1-\frac{x_1}{K_1}\right),\quad \frac{a_2}{f_2}(x_2)=K_2\left(A_2-\frac{x_2}{K_2}\right)$$

and

$$\left(\frac{a_1}{f_1}+g_2\right)(x_1)=\frac{K_1A_1}{b_{12}}-\frac{x_1}{b_{12}}(1-b_{12}b_{21}),\quad \left(\frac{a_2}{f_2}+g_1\right)(x_2)=K_2A_2.$$

Consequently, **(H1)**, **(H2)** and **(H3)** are satisfied, together with **(I1)** (see below for the exact expression of V_1). Since the existence of $\mathbf{E}^*$ is assured, as seen in [23], (1) fits our framework. Note that only one of $\frac{a_1}{f_1}+g_2$ and $\frac{a_2}{f_2}+g_1$ is strictly monotone in our settings.

Also, in this case,

$$V_1(x_1,x_2)=\frac{K_1b_{21}}{r_1b_{12}}\int_{x_1^*}^{x_1}\frac{\theta-x_1^*}{\theta}d\theta+\frac{K_2}{r_2}\int_{x_2^*}^{x_2}\frac{\theta-x_2^*}{\theta}d\theta=\frac{K_1b_{21}}{r_1b_{12}}\left[x_1^*\left(\frac{x_1}{x_1^*}-1-\ln\frac{x_1}{x_1^*}\right)+\frac{r_1b_{12}K_2}{r_2b_{21}K_1}x_2^*\left(\frac{x_2}{x_2^*}-1-\ln\frac{x_2}{x_2^*}\right)\right],$$

that is, V_1 differs from $\widetilde{L_2}$ by a multiplicative constant.

The Lyapunov functional V_1 given in (11) has been introduced by Harrison in [8] (up to a sign of one of the integrals, due to the different nature of the biological interactions involved) to discuss the stability of a predator–prey interaction. See also Korobeinikov [13,14], Georgescu and Hsieh [4] and Guo et al. [7] for a graph theoretic approach towards constructing Lyapunov functionals.

We now introduce the second set of auxiliary conditions, in the following form.

(H4) The functions a_2g_1 and a_1g_2 are strictly negative on $(0,\infty)$.
(H5) The functions $\frac{f_1}{a_1}+\frac{1}{g_2}$ and $\frac{f_2}{a_2}+\frac{1}{g_1}$ are monotone, both increasing if g_1,g_2 keep the same sign, or both decreasing if g_1,g_2 keep different signs. At least one of $\frac{f_1}{a_1}+\frac{1}{g_2}$ and $\frac{f_2}{a_2}+\frac{1}{g_1}$ is strictly monotone.
(I2) $\int_{x_i^*}^{\xi}\left(1-\frac{g_j(\theta)}{g_j(x_i^*)}\right)\frac{1}{a_i(\theta)}d\theta=+\infty$, for $\xi\in\{0,\infty\}$ and $(i,j)\in\{(1,2),(2,1)\}$.

We are now ready to state our second global stability result.
Theorem 3.2. *If* **(H1)**, **(H2)**, **(H4)**, **(H5)**, **(I2)** *and* **(E)** *are satisfied, then* $\mathbf{E}^*$ *is globally asymptotically stable in* $\mathrm{int}(\mathbb{R}_+^2)$.

Proof. We shall employ the following Lyapunov functional

$$V_2(x_1,x_2)=\int_{x_1^*}^{x_1}\left(1-\frac{g_2(\theta)}{g_2(x_1^*)}\right)\frac{1}{a_1(\theta)}d\theta+\int_{x_2^*}^{x_2}\left(1-\frac{g_1(\theta)}{g_1(x_2^*)}\right)\frac{1}{a_2(\theta)}d\theta. \tag{13}$$

First, it is seen that from **(H2)** and **(H4)** that V_2 increases whenever any of $|x_1-x_1^*|$ and $|x_2-x_2^*|$ increases and $V_2(x_1,x_2)\geqslant 0$ for all $x_1,x_2\geqslant 0$, while $V_2(x_1,x_2)=0$ if and only if $x_1=x_1^*$ and $x_2=x_2^*$. Also, by **(I2)**, $V_2(x_1,x_2)$ tends to $+\infty$ if either x_1 or x_2 tends to 0 or to $+\infty$. One then has

$$\begin{aligned}\dot V_2&=\left(1-\frac{g_2(x_1)}{g_2(x_1^*)}\right)\frac{1}{a_1(x_1)}(a_1(x_1)+f_1(x_1)g_1(x_2))+\left(1-\frac{g_1(x_1)}{g_1(x_2^*)}\right)\frac{1}{a_2(x_1)}(a_2(x_2)+f_2(x_2)g_2(x_1))\\&=\left(1-\frac{g_2(x_1)}{g_2(x_1^*)}\right)(-g_1(x_2))\left(-\frac{1}{g_1(x_2)}-\frac{f_1(x_1)}{a_1(x_1)}\right)+\left(1-\frac{g_1(x_2)}{g_1(x_2^*)}\right)(-g_2(x_1))\left(-\frac{1}{g_2(x_1)}-\frac{f_2(x_2)}{a_2(x_2)}\right)\end{aligned}$$

Using the equilibrium conditions (10), it is seen that

$$\begin{aligned}\dot V_2&=g_2(x_1)g_1(x_2)\left(-\frac{1}{g_2(x_1)}+\frac{1}{g_2(x_1^*)}\right)\left[-\frac{1}{g_1(x_2)}+\frac{1}{g_1(x_2^*)}-\frac{f_1(x_1)}{a_1(x_1)}+\frac{f_1(x_1^*)}{a_1(x_1^*)}\right]\\&\quad+g_2(x_1)g_1(x_2)\left(-\frac{1}{g_1(x_2)}+\frac{1}{g_1(x_2^*)}\right)\left[-\frac{1}{g_2(x_1)}+\frac{1}{g_2(x_1^*)}-\frac{f_2(x_2)}{a_2(x_2)}+\frac{f_2(x_2^*)}{a_2(x_2^*)}\right]\\&=g_2(x_1)g_1(x_2)\left[\left(-\frac{1}{g_2(x_1)}+\frac{1}{g_2(x_1^*)}\right)\left(-\frac{f_1(x_1)}{a_1(x_1)}+\frac{f_1(x_1^*)}{a_1(x_1^*)}\right)+\left(-\frac{1}{g_1(x_2)}+\frac{1}{g_1(x_2^*)}\right)\left(-\frac{f_2(x_2)}{a_2(x_2)}+\frac{f_2(x_2^*)}{a_2(x_2^*)}\right)\right.\\&\quad\left.+2\left(-\frac{1}{g_2(x_1)}+\frac{1}{g_2(x_1^*)}\right)\left(-\frac{1}{g_1(x_2)}+\frac{1}{g_1(x_2^*)}\right)\right].\end{aligned}$$

Having in view that $2ab\leqslant a^2+b^2$ for all $a,b\in\mathbb{R}$, one obtains that

$$\begin{aligned}\dot V_2&\leqslant\frac{g_1(x_2)}{g_2(x_1)}(g_2(x_1)-g_2(x_1^*))\left(-\frac{f_1(x_1)}{a_1(x_1)}-\frac{1}{g_2(x_1)}+\frac{f_1(x_1^*)}{a_1(x_1^*)}+\frac{1}{g_2(x_1^*)}\right)\\&\quad+\frac{g_2(x_1)}{g_1(x_2)}(g_1(x_2)-g_1(x_2^*))\left(-\frac{f_2(x_2)}{a_2(x_2)}-\frac{1}{g_1(x_2)}+\frac{f_2(x_2^*)}{a_2(x_2^*)}+\frac{1}{g_1(x_2^*)}\right).\end{aligned}$$

Noting that, by **(H2)** and **(H5)** $\dot V_2\leqslant 0$, with equality if and only if either $x_1=x_1^*$ or $x_2=x_2^*$ and, in any case, $\mathbf{E}^*$ is the only invariant set in $M=\left\{(x_1,x_2);\dot V_2(x_1,x_2)=0\right\}$, it follows by LaSalle's invariance theorem that $\mathbf{E}^*$ is globally asymptotically stable in $\mathrm{int}(\mathbb{R}_+^2)$.

Rearranging now the model (2) in the form

$$\begin{aligned}\frac{dx_1}{dt}&=r_1x_1A_1-\frac{r_1x_1^2}{K_1+b_{12}x_2}\\\frac{dx_2}{dt}&=r_2x_2A_2-\frac{r_2x_2x_2^2}{K_2+b_{21}x_1},\end{aligned} \tag{14}$$

one may choose

$$a_1(x_1)=r_1x_1A_1,\quad a_2(x_2)=r_2x_2A_2,\quad f_1(x_1)=\frac{r_1x_1^2}{b_{12}A_2},\quad g_1(x_2)=-\frac{b_{12}A_2}{K_1+b_{12}x_2},\quad f_2(x_2)=r_2x_2^2,\quad g_2(x_1)=-\frac{1}{K_2+b_{21}x_1}.$$

Assume also that (5) is satisfied. In this case,

$$\frac{f_1}{a_1}(x_1)=\frac{x_1}{A_1A_2b_{12}},\quad\frac{f_2}{a_2}(x_2)=\frac{x_2}{A_2}$$

and

$$\left(\frac{f_1}{a_1}+\frac{1}{g_2}\right)(x_1)=\frac{x_1(1-A_1A_2b_{12}b_{21})}{A_1A_2b_{12}}-K_2,\quad \left(\frac{f_2}{a_2}+\frac{1}{g_1}\right)(x_2)=-\frac{K_1}{b_{12}A_2}.$$

Consequently, **(H1)**, **(H2)**, **(H4)** and **(H5)** are satisfied, together with **(I2)** (see below for the exact expression of V_2). Since the existence of $\mathbf{E}^*$ is assured, as seen in [23], (2) fits our framework. Again, note that only one of $\frac{f_1}{a_1}+\frac{1}{g_2}$ and $\frac{f_2}{a_2}+\frac{1}{g_1}$ is strictly monotone and that our choice of parameters removes the need for the auxiliary condition (8).

Also, in this case,

$$\begin{aligned}V_2(x_1,x_2)&=\int_{x_1^*}^{x_1}\frac{b_{21}(\theta-x_1^*)}{K_2+b_{21}\theta}\frac{1}{r_1\theta A_1}d\theta+\int_{x_2^*}^{x_2}\frac{b_{12}(\theta-x_2^*)}{K_1+b_{12}\theta}\frac{1}{r_2\theta A_2}d\theta\\&=\frac{b_{21}}{r_1A_1}\left[\int_{x_1^*}^{x_1}\frac{\theta-x_1^*}{(K_2+b_{21}\theta)\theta}d\theta+\frac{b_{12}r_1A_1}{b_{21}r_2A_2}\int_{x_2^*}^{x_2}\frac{\theta-x_2^*}{(K_1+b_{12}\theta)\theta}d\theta\right],\end{aligned}$$

that is, V_2 differs from $\widetilde{L_1}$ by a multiplicative constant.

4. Global stability with less monotonicity and more positivity

We now discuss the global stability of $\mathbf{E}^*$ under weaker monotonicity properties than the key hypotheses **(H3)** and **(H5)** used above. Let us suppose that, apart from **(H1)** and **(H2)**, the following additional conditions are satisfied.

(P1) The functions g_1 and g_2 are strictly positive on $(0,\infty)$.

(P2) $\frac{f_1}{a_1}(0)>0, \frac{a_1}{f_1}(0)>0, \frac{f_2}{a_2}(0)>0, \frac{a_2}{f_2}(0)>0$ and $\frac{a_1}{f_1}(x_1)<\frac{a_1}{f_1}(0)$ for all $x_1>0, \frac{a_2}{f_2}(x_2)<\frac{a_2}{f_2}(0)$ for all $x_2>0$.

(I3) $\int_{x_i^*}^{\xi}\left(1-\frac{g_j(x_i^*)}{g_j(\theta)}\right)\frac{1}{f_i(\theta)}d\theta=+\infty$, for $\xi\in\{0,\infty\}$and $(i,j)\in\{(1,2),(2,1)\}$.

Note that if **(H3)** holds, then necessarily $\frac{a_1}{f_1}$ and $\frac{a_2}{f_2}$ are strictly decreasing, and consequently the second part of **(P2)** holds. Also, condition **(P2)** implies the positivity of a_1 and a_2 in a vicinity of the origin. Combined with **(P1)** and **(H1)**, this precludes our model from representing an obligate mutualism. Define the functions $\eta_1,\eta_2:[0,\infty)\to\mathbb{R}$ by

$$\eta_1(x_1)=1-\frac{a_1}{f_1}(x_1)\frac{f_1}{a_1}(0),\quad \eta_2(x_2)=1-\frac{a_2}{f_2}(x_2)\frac{f_2}{a_2}(0) \tag{15}$$

and remark that, due to **(P2)**, η_1 and η_2 are strictly positive on $(0,\infty)$. Let us now employ the Lyapunov functional V_3 defined by

$$V_3(x_1,x_2)=\int_{x_1^*}^{x_1}\left(1-\frac{g_2(x_1^*)}{g_2(\theta)}\right)\frac{1}{f_1(\theta)}d\theta+\left[\int_{x_2^*}^{x_2}\left(1-\frac{g_1(x_2^*)}{g_1(\theta)}\right)\frac{1}{f_2(\theta)}d\theta\right]\frac{g_1(x_2^*)}{g_2(x_1^*)}. \tag{16}$$

We now compute the time derivative of V_3 along the solutions of (9).

Lemma 4.1. *The time derivative of V_3 along the solutions of (9) is*

$$\begin{aligned}\dot V_3=&\left(1-\frac{g_2(x_1^*)}{g_2(x_1)}\right)\frac{a_1}{f_1}(0)\left(1-\frac{g_2(x_1)}{g_2(x_1^*)}\right)+\left(1-\frac{g_1(x_2^*)}{g_1(x_2)}\right)\frac{a_2}{f_2}(0)\left(1-\frac{g_1(x_2)}{g_1(x_2^*)}\right)\frac{g_1(x_2^*)}{g_2(x_1^*)}\\&+g_1(x_2^*)\left(2-\frac{g_1(x_2)}{g_1(x_2^*)}\frac{g_2(x_1^*)}{g_2(x_1)}-\frac{g_1(x_2^*)}{g_1(x_2)}\frac{g_2(x_1)}{g_2(x_1^*)}\right)+\left(1-\frac{g_2(x_1^*)}{g_2(x_1)}\right)g_1(x_2^*)\eta_1(x_1)\left(\frac{g_2(x_1)}{g_2(x_1^*)}\frac{\eta_1(x_1^*)}{\eta_1(x_1)}-1\right)\\&+\left(1-\frac{g_1(x_2^*)}{g_1(x_2)}\right)g_1(x_2^*)\eta_2(x_2)\left(\frac{g_1(x_2)}{g_1(x_2^*)}\frac{\eta_2(x_2^*)}{\eta_2(x_2)}-1\right)\end{aligned} \tag{17}$$

Proof. One sees that

$$\begin{aligned}\dot V_3&=\left(1-\frac{g_2(x_1^*)}{g_2(x_1)}\right)\left(\frac{a_1}{f_1}(x_1)+g_1(x_2)\right)+\left(1-\frac{g_1(x_2^*)}{g_1(x_2)}\right)\left(\frac{a_2}{f_2}(x_2)+g_2(x_1)\right)\frac{g_1(x_2^*)}{g_2(x_1^*)}\\&=\left(1-\frac{g_2(x_1^*)}{g_2(x_1)}\right)\frac{a_1}{f_1}(0)\left[\left(\frac{a_1}{f_1}(x_1)\frac{f_1}{a_1}(0)+g_1(x_2)\frac{f_1}{a_1}(0)\right)\right]+\left(1-\frac{g_1(x_2^*)}{g_1(x_2)}\right)\frac{a_2}{f_2}(0)\left[\left(\frac{a_2}{f_2}(x_2)\frac{f_2}{a_2}(0)+g_2(x_1)\frac{f_2}{a_2}(0)\right)\right]\frac{g_2(x_1^*)}{g_2(x_1^*)}\\&=E_1+E_2.\end{aligned}$$

It follows that

$$E_1=\left(1-\frac{g_2(x_1^*)}{g_2(x_1)}\right)\frac{a_1}{f_1}(0)\left(1-\frac{g_2(x_1)}{g_2(x_1^*)}\right)+\left(1-\frac{g_2(x_1^*)}{g_2(x_1)}\right)\frac{a_1}{f_1}(0)\left[-1+\frac{g_2(x_1)}{g_2(x_1^*)}+\frac{a_1}{f_1}(x_1)\frac{f_1}{a_1}(0)+g_1(x_2)\frac{f_1}{a_1}(0)\right]=E_{11}+E_{12}$$

where

$$E_{11} = \left(1 - \frac{g_2(x_1^*)}{g_2(x_1)}\right) \frac{a_1}{f_1}(0) \left(1 - \frac{g_2(x_1)}{g_2(x_1^*)}\right) \tag{18}$$

and

$$\begin{aligned} E_{12} &= \left(1 - \frac{g_2(x_1^*)}{g_2(x_1)}\right) g_1(x_2^*) \left[\left(\frac{g_2(x_1)}{g_2(x_1^*)} - \eta_1(x_1)\right) \frac{a_1}{f_1}(0) \frac{1}{g_1(x_2^*)} + \frac{g_1(x_2)}{g_1(x_2^*)}\right] \\ &= \left(1 - \frac{g_2(x_1^*)}{g_2(x_1)}\right) g_1(x_2^*) \left[\eta_1(x_1) \left(\frac{g_2(x_1)}{g_2(x_1^*)} \frac{1}{\eta_1(x_1)} - 1\right) \frac{a_1}{f_1}(0) \frac{1}{g_1(x_2^*)} + \frac{g_1(x_2)}{g_1(x_2^*)}\right]. \end{aligned} \tag{19}$$

Similarly,

$$\begin{aligned} E_2 &= \left(1 - \frac{g_1(x_2^*)}{g_1(x_2)}\right) \frac{a_2}{f_2}(0) \left(1 - \frac{g_1(x_2)}{g_1(x_2^*)}\right) \frac{g_1(x_2^*)}{g_2(x_1^*)} + \left(1 - \frac{g_1(x_2^*)}{g_1(x_2)}\right) \frac{a_2}{f_2}(0) \left[-1 + \frac{g_1(x_2)}{g_1(x_2^*)} + \frac{a_2}{f_2}(x_2) \frac{f_2}{a_2}(0) + g_2(x_1) \frac{f_2}{a_2}(0)\right] \frac{g_1(x_2^*)}{g_2(x_1^*)} \\ &= E_{21} + E_{22}, \end{aligned}$$

where

$$E_{21} = \left(1 - \frac{g_1(x_2^*)}{g_1(x_2)}\right) \frac{a_2}{f_2}(0) \left(1 - \frac{g_1(x_2)}{g_1(x_2^*)}\right) \frac{g_1(x_2^*)}{g_2(x_1^*)} \tag{20}$$

and

$$\begin{aligned} E_{22} &= \left(1 - \frac{g_1(x_2^*)}{g_1(x_2)}\right) g_1(x_2^*) \left[\left(\frac{g_1(x_2)}{g_1(x_2^*)} - \eta_2(x_2)\right) \frac{a_2}{f_2}(0) \frac{1}{g_2(x_1^*)} + \frac{g_2(x_1)}{g_2(x_1^*)}\right] \\ &= \left(1 - \frac{g_1(x_2^*)}{g_1(x_2)}\right) g_1(x_2^*) \left[\eta_2(x_2) \left(\frac{g_1(x_2)}{g_1(x_2^*)} \frac{1}{\eta_2(x_2)} - 1\right) \frac{a_2}{f_2}(0) \frac{1}{g_2(x_1^*)} + \frac{g_2(x_1)}{g_2(x_1^*)}\right]. \end{aligned} \tag{21}$$

Using the equilibrium conditions (10), it is seen that

$$-\frac{a_1(x_1^*)}{f_1(x_1^*)} \frac{f_1}{a_1}(0) = g_1(x_2^*) \frac{f_1}{a_1}(0), \quad -\frac{a_2(x_2^*)}{f_2(x_2^*)} \frac{f_2}{a_2}(0) = g_2(x_1^*) \frac{f_2}{a_2}(0)$$

and consequently

$$1 = \eta_1(x_1^*) - g_1(x_2^*) \frac{f_1}{a_1}(0), \quad 1 = \eta_2(x_2^*) - g_2(x_1^*) \frac{f_2}{a_2}(0). \tag{22}$$

One then sees from (19) and (22) that

$$E_{12} = \left(1 - \frac{g_2(x_1^*)}{g_2(x_1)}\right) g_1(x_2^*) \left[\eta_1(x_1) \left(\frac{g_2(x_1)}{g_2(x_1^*)} \frac{\eta_1(x_1^*)}{\eta_1(x_1)} - 1\right) - \frac{g_2(x_1)}{g_2(x_1^*)} + \frac{g_1(x_2)}{g_1(x_2^*)}\right] \tag{23}$$

and similarly

$$E_{22} = \left(1 - \frac{g_1(x_2^*)}{g_1(x_2)}\right) g_1(x_2^*) \left[\eta_2(x_2) \left(\frac{g_1(x_2)}{g_1(x_2^*)} \frac{\eta_2(x_2^*)}{\eta_2(x_2)} - 1\right) - \frac{g_1(x_2)}{g_1(x_2^*)} + \frac{g_2(x_1)}{g_2(x_1^*)}\right]. \tag{24}$$

It follows from (18), (20), (23) and (24) that

$$\begin{aligned} \dot{V}_3 &= \left(1 - \frac{g_2(x_1^*)}{g_2(x_1)}\right) \frac{a_1}{f_1}(0) \left(1 - \frac{g_2(x_1)}{g_2(x_1^*)}\right) + \left(1 - \frac{g_1(x_2^*)}{g_1(x_2)}\right) \frac{a_2}{f_2}(0) \left(1 - \frac{g_1(x_2)}{g_1(x_2^*)}\right) \frac{g_1(x_2^*)}{g_2(x_1^*)} \\ &\quad + \left(1 - \frac{g_2(x_1^*)}{g_2(x_1)}\right) g_1(x_2^*) \left[\eta_1(x_1) \left(\frac{g_2(x_1)}{g_2(x_1^*)} \frac{\eta_1(x_1^*)}{\eta_1(x_1)} - 1\right) - \frac{g_2(x_1)}{g_2(x_1^*)} + \frac{g_1(x_2)}{g_1(x_2^*)}\right] \\ &\quad + \left(1 - \frac{g_1(x_2^*)}{g_1(x_2)}\right) g_1(x_2^*) \left[\eta_2(x_2) \left(\frac{g_1(x_2)}{g_1(x_2^*)} \frac{\eta_2(x_2^*)}{\eta_2(x_2)} - 1\right) - \frac{g_1(x_2)}{g_1(x_2^*)} + \frac{g_2(x_1)}{g_2(x_1^*)}\right], \end{aligned}$$

which easily yields the conclusion.

Due to the positivity conditions **(P1)** and **(P2)**, the first two terms in the right-hand side of (17) are negative (with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$, respectively), while the third is negative due to **(P1)** and to *AM–GM* inequality. Let us also observe that, by **(I3)**, $V_3(x_1, x_2)$ tends to $+\infty$ if either x_1 or x_2 tends to 0 or to $+\infty$. Denote

$$\Phi_1(x_1) = \frac{g_2(x_1)}{\eta_1(x_1)}, \quad \Phi_2(x_2) = \frac{g_1(x_2)}{\eta_2(x_2)}. \tag{25}$$

One then sees that the sum of the fourth and fifth terms in the right-hand side of (17) can be written as

$$T_4+T_5=g_1(x_2^*)\left(1-\frac{g_2(x_1^*)}{g_2(x_1)}\right)\eta_1(x_1)\left(\frac{\Phi_1(x_1)}{\Phi_1(x_1^*)}-1\right)+g_1(x_2^*)\left(1-\frac{g_1(x_2^*)}{g_1(x_2)}\right)\eta_2(x_2)\left(\frac{\Phi_2(x_2)}{\Phi_2(x_2^*)}-1\right).$$

By using an argument similar to the one displayed in the proof of Theorems 3.1 and 3.2, one then obtains the following stability result.

Theorem 4.1. *If* **(H1)**, **(H2)**, **(P1)**, **(P2)**, **(I3)** *and* **(E)** *are satisfied, and*

$$g_1(x_2^*)\left(1-\frac{g_2(x_1^*)}{g_2(x_1)}\right)\eta_1(x_1)\left(\frac{\Phi_1(x_1)}{\Phi_1(x_1^*)}-1\right)+g_1(x_2^*)\left(1-\frac{g_1(x_2^*)}{g_1(x_2)}\right)\eta_2(x_2)\left(\frac{\Phi_2(x_2)}{\Phi_2(x_2^*)}-1\right)\leqslant 0,\ \text{for all } x_1,x_2>0, \tag{26}$$

then $\mathbf{E}^*$ *is globally asymptotically stable in* $\mathrm{int}(\mathbb{R}_+^2)$.

Note that (26) is satisfied, for instance, if Φ_1 and Φ_2 are decreasing.

For

$$a_1(x_1)=r_1x_1\left(A_1-\frac{x_1}{K_1}\right),\quad a_2(x_2)=r_2x_2\left(A_2-\frac{x_2}{K_2}\right),\quad f_1(x_1)=x_1,\quad g_1(x_2)=\frac{r_1b_{12}x_2}{K_1},\quad f_2(x_2)=x_2,\quad g_2(x_1)=\frac{r_2b_{21}x_1}{K_2},$$

assuming that either (3) or (4) are satisfied, it follows that **(E)** holds, together with **(H1)**, **(H2)**, **(I3)** (see below for the exact expression of V_3) and **(P1)**. Also,

$$\frac{a_1}{f_1}(x_1)=r_1\left(A_1-\frac{x_1}{K_1}\right),\quad \frac{a_2}{f_2}(x_2)=r_2\left(A_2-\frac{x_2}{K_2}\right),\quad \eta_1(x_1)=\frac{x_1}{A_1K_1},\quad \eta_2(x_2)=\frac{x_2}{A_2K_2},\quad \Phi_1(x_1)=r_2b_{21}A_1,\quad \Phi_2=r_1b_{12}A_2,$$

and consequently **(P2)** and (26) hold. It follows that the model (1) fits our framework.

Also, in this case,

$$V_3(x_1,x_2)=\int_{x_1^*}^{x_1}\left(1-\frac{x_1^*}{\theta}\right)\frac{1}{\theta}d\theta+\frac{r_1b_{12}K_2x_2^*}{r_2b_{21}K_1x_1^*}\left(\int_{x_2^*}^{x_2}\left(1-\frac{x_2^*}{\theta}\right)\frac{1}{\theta}d\theta\right)=\left(\ln\frac{x_1}{x_1^*}+\frac{x_1^*}{x_1}-1\right)+\frac{r_1b_{12}K_2x_2^*}{r_2b_{21}K_1x_1^*}\left(\ln\frac{x_2}{x_2^*}+\frac{x_2^*}{x_2}-1\right),$$

that is, V_3 differs from L_2 by a multiplicative constant.

Let us now suppose that the following conditions are satisfied.

(P3) The functions g_1 and g_2 keep the same sign on $(0,\infty), g_1(0)\neq 0$ and $g_2(0)\neq 0$.
(P4) The functions $\frac{a_1}{f_1}$ and $\frac{a_2}{f_2}$ are decreasing on $[0,\infty)$, at least one of them being strictly decreasing.

Note that if **(P3)** and **(H5)** hold, then **(P4)** holds.

Let us denote

$$\xi_1(x_2)=\frac{1}{g_1(0)}-\frac{1}{g_1(x_2)},\quad \xi_2(x_1)=\frac{1}{g_2(0)}-\frac{1}{g_2(x_1)}$$

and observe that ξ_1,ξ_2 are increasing and $\xi_1(x_2)>0$ for all $x_2>0, \xi_2(x_1)>0$ for all $x_1>0$. Let us also denote

$$\Psi_1(x_2)=\frac{\xi_1a_2}{f_2}(x_2),\quad \Psi_2(x_1)=\frac{\xi_2a_1}{f_1}(x_1).$$

One shall employ again the Lyapunov functional V_1. Using the equilibrium condition (10), one sees that

$$\begin{aligned}\dot V_1&=\frac{g_2(x_1)-g_2(x_1^*)}{f_1(x_1)}(a_1(x_1)+f_1(x_1)g_1(x_2))+\frac{g_1(x_2)-g_1(x_2^*)}{f_2(x_2)}(a_2(x_2)+f_2(x_2)g_2(x_1))\\
&=(g_2(x_1)-g_2(x_1^*))(-g_1(x_2))\left(-\frac{1}{g_1(x_2)}\frac{a_1(x_1)}{f_1(x_1)}+\frac{1}{g_1(x_2^*)}\frac{a_1(x_1^*)}{f_1(x_1^*)}\right)\\
&\quad+(g_1(x_2)-g_1(x_2^*))(-g_2(x_1))\left(-\frac{1}{g_2(x_1)}\frac{a_2(x_2)}{f_2(x_2)}+\frac{1}{g_2(x_1^*)}\frac{a_2(x_2^*)}{f_2(x_2^*)}\right)\\
&=(g_2(x_1)-g_2(x_1^*))(-g_1(x_2))\cdot\left[-\frac{1}{g_1(0)}\left(\frac{a_1(x_1)}{f_1(x_1)}-\frac{a_1(x_1^*)}{f_1(x_1^*)}\right)+\xi_1(x_2)\frac{a_1(x_1)}{f_1(x_1)}-\xi_1(x_2^*)\frac{a_1(x_1^*)}{f_1(x_1^*)}\right]\\
&\quad+(g_1(x_2)-g_1(x_2^*))(-g_2(x_1))\cdot\left[-\frac{1}{g_2(0)}\left(\frac{a_2(x_2)}{f_2(x_2)}-\frac{a_2(x_2^*)}{f_2(x_2^*)}\right)+\xi_2(x_1)\frac{a_2(x_2)}{f_2(x_2)}-\xi_2(x_1^*)\frac{a_2(x_2^*)}{f_2(x_2^*)}\right].\end{aligned}$$

Consequently,

$$\begin{aligned}\dot{V}_1 &= (g_2(x_1)-g_2(x_1^*))\frac{g_1(x_2)}{g_1(0)}\left[\frac{a_1(x_1)}{f_1(x_1)}-\frac{a_1(x_1^*)}{f_1(x_1^*)}\right]+(g_1(x_2)-g_1(x_2^*))\frac{g_2(x_1)}{g_2(0)}\left[\frac{a_2(x_2)}{f_2(x_2)}-\frac{a_2(x_2^*)}{f_2(x_2^*)}\right]\\ &\quad+(g_2(x_1)-g_2(x_1^*))(-g_1(x_2))\left[\xi_1(x_2)\frac{a_1(x_1)}{f_1(x_1)}-\xi_1(x_2^*)\frac{a_1(x_1^*)}{f_1(x_1^*)}\right]\\ &\quad+(g_1(x_2)-g_1(x_2^*))(-g_2(x_1))\left[\xi_2(x_1)\frac{a_2(x_2)}{f_2(x_2)}-\xi_2(x_1^*)\frac{a_2(x_2^*)}{f_2(x_2^*)}\right]\\ &= T_1+T_2+T_3+T_4\end{aligned}$$

It is now seen using **(P4)** that T_1 and T_2 are negative. Let us note that, using again the equilibrium conditions (10), that

$$\begin{aligned}T_3+T_4 &= g_2(x_1)g_1(x_2)\frac{a_2(x_2^*)}{f_2(x_2^*)}(\xi_2(x_1)-\xi_2(x_1^*))\left(\xi_1(x_2)\frac{a_1(x_1)}{f_1(x_1)}-\xi_1(x_2^*)\frac{a_1(x_1^*)}{f_1(x_1^*)}\right)+g_1(x_2)g_2(x_1)\frac{a_1(x_1^*)}{f_1(x_1^*)}(\xi_1(x_2)\\ &\qquad -\xi_1(x_2^*))\left(\xi_2(x_1)\frac{a_2(x_2)}{f_2(x_2)}-\xi_2(x_1^*)\frac{a_2(x_2^*)}{f_2(x_2^*)}\right)\\ &= g_2(x_1)g_1(x_2)\frac{a_1(x_1^*)}{f_1(x_1^*)}\frac{a_2(x_2^*)}{f_2(x_2^*)}\xi_1(x_2^*)\xi_2(x_1^*)\\ &\quad\cdot\left[\left(\frac{\xi_2(x_1)}{\xi_2(x_1^*)}-1\right)\left(\frac{\xi_1(x_2)}{\xi_1(x_2^*)}\frac{f_1(x_1^*)}{a_1(x_1^*)}\frac{a_1(x_1)}{f_1(x_1)}-1\right)+\left(\frac{\xi_1(x_2)}{\xi_1(x_2^*)}-1\right)\left(\frac{\xi_2(x_1)}{\xi_2(x_1^*)}\frac{f_2(x_2^*)}{a_2(x_2^*)}\frac{a_2(x_2)}{f_2(x_2)}-1\right)\right]\\ &= g_2(x_1)g_1(x_2)\Psi_2(x_1^*)\Psi_1(x_2^*)\\ &\quad\cdot\left[\frac{\xi_1(x_2)}{\xi_1(x_2^*)}\left(\frac{\Psi_2(x_1)}{\Psi_2(x_1^*)}-1\right)+\frac{\xi_2(x_1)}{\xi_2(x_1^*)}\left(\frac{\Psi_1(x_2)}{\Psi_1(x_2^*)}-1\right)+2-\frac{\xi_1(x_2)}{\xi_1(x_2^*)}\frac{\xi_2(x_1^*)}{\xi_2(x_1)}\frac{\Psi_2(x_1)}{\Psi_2(x_1^*)}-\frac{\xi_2(x_1)}{\xi_2(x_1^*)}\frac{\xi_1(x_2^*)}{\xi_1(x_2)}\frac{\Psi_1(x_2)}{\Psi_1(x_2^*)}\right]\end{aligned}$$

By **(P3)** and **(P4)**, it is seen that

$$g_2(x_1)g_1(x_2)\Psi_2(x_1^*)\Psi_1(x_2^*)>0 \quad \text{for } x_1,x_2\in(0,\infty).$$

By using again an argument similar to the one displayed in the proof of Theorems 3.1 and 3.2, one then obtains the following stability result.

Theorem 4.2. *If* **(H1)**, **(H2)**, **(P3)**, **(P4)**, **(I1)** *and* **(E)** *are satisfied, and*

$$\frac{\xi_1(x_2)}{\xi_1(x_2^*)}\left(\frac{\Psi_2(x_1)}{\Psi_2(x_1^*)}-1\right)+\frac{\xi_2(x_1)}{\xi_2(x_1^*)}\left(\frac{\Psi_1(x_2)}{\Psi_1(x_2^*)}-1\right)+2-\frac{\xi_1(x_2)}{\xi_1(x_2^*)}\frac{\xi_2(x_1^*)}{\xi_2(x_1)}\frac{\Psi_2(x_1)}{\Psi_2(x_1^*)}-\frac{\xi_2(x_1)}{\xi_2(x_1^*)}\frac{\xi_1(x_2^*)}{\xi_1(x_2)}\frac{\Psi_1(x_2)}{\Psi_1(x_2^*)}\leqslant 0,\ \text{for all } x_1,x_2>0, \tag{27}$$

then $\mathbf{E}^*$ *is globally asymptotically stable in* $\mathrm{int}(\mathbb{R}^2_+)$.

Let us observe that for $x_1=x_1^*$ and all $x_2>0$

$$\begin{aligned}T_3+T_4 &= g_2(x_1)g_1(x_2)\Psi_2(x_1^*)\Psi_1(x_2^*)\left[\frac{\Psi_1(x_2)}{\Psi_1(x_2^*)}+1-\frac{\xi_1(x_2)}{\xi_1(x_2^*)}-\frac{\xi_1(x_2^*)}{\xi_1(x_2)}\frac{\Psi_1(x_2)}{\Psi_1(x_2^*)}\right]\\ &= g_2(x_1)g_1(x_2)\Psi_2(x_1^*)\Psi_1(x_2^*)\left(\frac{\Psi_1(x_2)}{\Psi_1(x_2^*)}-\frac{\xi_1(x_2)}{\xi_1(x_2^*)}\right)\left(1-\frac{\xi_1(x_2)}{\xi_1(x_2^*)}\right)\\ &= g_2(x_1)g_1(x_2)\Psi_2(x_1^*)\left(\frac{a_2(x_2)}{f_2(x_2)}-\frac{a_2(x_2^*)}{f_2(x_2^*)}\right)(\xi_1(x_2)-\xi_1(x_2^*))\leqslant 0.\end{aligned}$$

Similarly, for $x_2=x_2^*$ and all $x_1>0$,

$$T_3+T_4=g_2(x_1)g_1(x_2)\Psi_1(x_2^*)\left(\frac{a_1(x_1)}{f_1(x_1)}-\frac{a_1(x_1^*)}{f_1(x_1^*)}\right)(\xi_2(x_1)-\xi_2(x_1^*))\leqslant 0,$$

that is, (27) is easily satisfied. For

$$a_1(x_1)=r_1x_1A_1,\quad a_2(x_2)=r_2x_2A_2,\quad f_1(x_1)=r_1x_1^2,\quad g_1(x_2)=-\frac{1}{K_1+b_{12}x_2},\quad f_2(x_2)=r_2x_2^2,\quad g_2(x_1)=-\frac{1}{K_2+b_{21}x_1},$$

and assuming also that (5) is satisfied, one obtains

$$\xi_1(x_2)=b_{12}x_2,\quad \xi_2(x)=b_{21}x_1,\quad \Psi_1(x_2)=b_{12}A_2,\quad \Psi_2(x_1)=b_{21}A_1$$

and

$$T_3+T_4=\frac{A_1A_2}{(K_1+b_{12}x_2)(K_2+b_{21}x_1)}b_{12}b_{21}\left(2-\frac{x_2x_1^*}{x_2^*x_1}-\frac{x_1x_2^*}{x_1^*x_2}\right)\leqslant 0,$$

due to the $AM - GM$ inequality, so the model (2) fits also this framework. Also, in this case,

$$V_1(x_1,x_2) = \int_{x_1^*}^{x_1} \frac{\frac{1}{K_2+b_{21}x_1^*} - \frac{1}{K_2+b_{21}\theta}}{r_1\theta^2} d\theta + \int_{x_2^*}^{x_2} \frac{\frac{1}{K_1+b_{12}x_2^*} - \frac{1}{K_1+b_{12}\theta}}{r_2\theta^2} d\theta$$
$$= \frac{A_2 b_{21}}{x_2^* r_1}\left[\int_{x_1^*}^{x_1} \frac{\theta - x_2^*}{(K_2+b_{21}\theta)\theta^2} d\theta + \frac{r_1 A_1 b_{12} x_2^*}{r_2 A_2 b_{21} x_1^*}\int_{x_2^*}^{x_2} \frac{\theta - x_2^*}{(K_1+b_{12}\theta)\theta^2} d\theta\right],$$

that is, V_1 differs from L_1 by a multiplicative constant.

Although (26) and (27) are tailored to the (general form of) systems (1) and (2) through the specific construction of η_1, η_2, ξ_1 and ξ_2, respectively, they are satisfied for other related models as well. Specifically, (26) is also satisfied for the model

$$\frac{dx_1}{dt} = r_1 x_1\left(A_1 - \left(\frac{x_1}{K_1}\right)^p\right) + r_1\frac{b_{12}}{K_1}x_1x_2, \quad \frac{dx_2}{dt} = r_2 x_2\left(A_2 - \left(\frac{x_2}{K_2}\right)^p\right) + r_2\frac{b_{21}}{K_2}x_1x_2,$$

(that is, for a version of (1) featuring a Richards growth function instead of the logistic one), provided that $p \geqslant 1$. Also, (27) is satisfied for the model

$$\frac{dx_1}{dt} = r_1x_1A_1 - \frac{r_1x_1^{p+1}}{K_1 + b_{12}x_2^p}$$
$$\frac{dx_2}{dt} = r_2x_2A_2 - \frac{r_2x_2x_2^{p+1}}{K_2 + b_{21}x_1^p},$$

(that is, for a version of (2) featuring a more general interaction term), provided that $p > 0$. Further, the model with restricted growth rates

$$\frac{dx_1}{dt} = r_1x_1\left(1 - \frac{x_1}{K_1}\right) + c_1x_1(1 - e^{-\alpha_2 x_2}), \quad \frac{dx_2}{dt} = r_2x_2\left(1 - \frac{x_2}{K_2}\right) + c_2x_2(1 - e^{-\alpha_1 x_1}),$$

proposed by Graves et al. in [6] can be treated within the framework of both Theorem 3.1 and Theorem 4.1.

When (26) and (27) are satisfied only for (x_1, x_2) in a vicinity of $\mathbf{E}^*$ rather than globally, our Theorems 4.1 and 4.2 can be restated in terms of finding domains of attraction for $\mathbf{E}^*$. Another possible way for extending the scope of our results is considering models of mutualism with more complicated, possibly sign changing, interaction terms between species, such as the system

$$\frac{dA}{dt} = (r_aF - d_aA)A, \quad \frac{dF}{dt} = \left(\frac{r_f aA^2}{b + aA^2}d_fF - r_cA\right)F,$$

proposed by Kang et al. in [15] to model the interactions between leaf-cutter ants (A) and their fungus garden (F), although, under a strict definition, this interaction does not always represent a mutualism, being detrimental for the fungus for certain species densities. This model showcases a general class of models, called, in the unifying framework of Holland and DeAngelis [11], unidirectional consumer-resource mutualisms, in which one species is dependent on the other one for survival, while being also its primary source of nutrient.

Acknowledgments

The authors are indebted to an unknown referee for insightful remarks and for pointing us to the references [2], [24]. The work of P. Georgescu was supported by a grant of the Romanian National Authority for Scientific Research, CNCS-UEFISCDI, project number PN-II-ID-PCE-2011–3-0557. The work of H. Zhang was supported by the National Natural Science Foundation of China, Grant IDs 11126142 and 11201187.

References

[1] J. Addicott, Stability properties of 2-species models of mutualism: simulation studies, Oecologia 49 (1981) 42–49.
[2] F. Bäckhed, R.E. Ley, J.L. Sonnenburg, D.A. Peterson, J.I. Gordon, Host-bacterial mutualism in the human intestine, Science 307 (2005) 1915–1920.
[3] J.L. Bronstein, Conditional outcomes in mutualistic interactions, Trends Ecol. Evol. 9 (1994) 214–217.
[4] P. Georgescu, Y.-H. Hsieh, Global stability for a virus dynamics model with nonlinear incidence of infection and removal, SIAM J. Appl. Math. 67 (2006) 337–353.
[5] B.S. Goh, Stability in models of mutualism, Am. Nat. 113 (1979) 261–275.
[6] W.G. Graves, B. Peckham, J. Pastor, A bifurcation analysis of a differential equations model for mutualism, Bull. Math. Biol. 68 (2006) 1851–1872.
[7] H. Guo, M.Y. Li, Z. Shuai, A graph-theoretic approach to the method of Lyapunov functions, Proc. Amer. Math. Soc. 136 (2008) 2793–2802.
[8] G.W. Harrison, Global stability of predator-prey interactions, J. Math. Biol. 8 (1979) 159–171.
[9] E.R. Heithaus, D.C. Culver, A.J. Beattie, Models of some ant–plant mutualisms, Am. Nat. 116 (1980) 347–361.
[10] M.-J. Hernandez, Dynamics of transitions between population interactions: a nonlinear interaction α-function defined, Proc. R. Soc. Lond. B 265 (1998) 1432–1440.

[11] J.N. Holland, D.L. DeAngelis, A consumer-resource approach to the density-dependent population dynamics of mutualism, Ecology 91 (2010) 1286–1295.
[12] D.H. Lewis, Mutualistic lives, Nature 297 (1982) 176.
[13] A. Korobeinikov, Lyapunov functions and global properties for SEIR and SEIS epidemic models, Math. Med. Biol. 21 (2004) 75–83.
[14] A. Korobeinikov, Lyapunov functions and global stability for SIR and SIRS epidemiological models with non-linear transmission, Bull. Math. Biol. 30 (2006) 615–626.
[15] Y. Kang, R. Clark, M. Makiyama, J. Fewell, Mathematical modeling on obligate emutualism: interactions between leaf-cutter ants and their fungus garden, J. Theor. Biol. 289 (2011) 116–127.
[16] M. Kot, Elements of Mathematical Ecology, Cambridge University Press, 2001.
[17] L. Margulis, Symbiosis and evolution, Sci. Am. 225 (1971) 49–55.
[18] R. May, Stability and Complexity in Model Ecosystems, Princeton University Press, Princeton, NJ, 1973.
[19] C.J. Melián, J. Bascompte, P. Jordano, V. Krivan, Diversity in a complex ecological network with two interaction types, Oikos 118 (2009) 122–130.
[20] J. Pastor, Mathematical Ecology of Populations and Ecosystems, Blackwell, Oxford, 2008.
[21] M. Ringel, H. Hu, G. Anderson, The stability and persistence of mutualisms embedded in community interactions, Theor. Popul. Biol. 50 (1996) 281–297.
[22] J. Vandermeer, D. Boucher, Varieties of mutualistic interaction in population models, J. Theor. Biol. 74 (1978) 549–558.
[23] C. Vargas-De-León, Lyapunov functions for two-species cooperative systems, Appl. Math. Comput. 219 (2012) 2493–2497.
[24] C. Vargas-De-León, G. Gómez-Alcaraz, Global stability in some ecological models of commensalism between two species, Biomatemática 23 (2013) 139–146.
[25] C. Wolin, L. Lawlor, Models of facultative mutualism: density effects, Am. Nat. 124 (1984) 843–862.