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THE GLOBAL STABILITY OF COEXISTING EQUILIBRIA FOR THREE MODELS OF MUTUALISM

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Abstract. We analyze the dynamics of three models of mutualism, establishing the global stability of coexisting equilibria by means of Lyapunov's second method. This further establishes the usefulness of certain Lyapunov functionals of an abstract nature introduced in an earlier paper. As a consequence, it is seen that the use of higher order self-limiting terms cures the shortcomings of Lotka-Volterra mutualisms, preventing unbounded growth and promoting global stability.

1. Introduction.

As seen in Holland and Bronstein [12], interactions between populations of different species can be classified, by the perceived positive (+), neutral (0) or negative (–) effects of each species on the other, into six types: mutualism (+ +), predation (+ –), commensalism (+ 0), neutralism (0 0), ammensalism (0 –) and competition (– –). In this regard, a mutualistic interaction of two species is then an association which benefits both.

Mutualisms usually involve the exchange of resources between species, each of them trading a resource to which it has easy access for another one difficult to acquire. For instance, most terrestrial plants rely on mycorrizal fungi for the uptake of phosphorus, providing carbon in return, while making available nectar and fruits to insects in exchange for pollination and seed transportation, respectively. Other common mutualisms involve protection from natural enemies or from unfavorable environmental conditions. For instance, acacia ants (*Pseudomyrmex ferruginea*) defend the bull-horn acacia (*Acacia cornigera*) from browsing by herbivores in exchange for nutrients and sheltering (Palmer *et al.* [20]).

Mutualisms are of key importance for the apparition of ancient eukaryotic cells, as chloroplasts and mitochondria were initially independent organisms. They are also a major source of new traits, since entire organisms can be acquired, the traits

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gained in this way being more complex than those obtained by transfer of isolated genes (Douglas [3]). Further, all living organisms are currently believed to take part in a mutualistic association at some point in their lives, some in as many as hundreds (Bronstein *et al.* [2]).

If neither species can survive without the other, as it is the case with the pairing between acacia ants and bull-horn acacia, the mutualism is called obligate, while if each species can survive on their own, the mutualism is called facultative. For instance, a plant that is subject to successful self-pollination or cross-pollination, while also being pollinated by multiple insects, is involved in facultative mutualisms with them.

A central paradigm of modern ecological thinking being the Darwinian theory of natural selection, the antagonistic interactions (predation and competition) received a far greater attention. The fact that the Lotka-Volterra model of mutualism, in which the interspecies competition terms have their sign changed from negative to positive, does normally have unbounded solutions unless the interspecies interaction is weak or asymmetric, probably also helped convey the idea that mutualisms are of less importance. May [17] noted that Lotka-Volterra models are totally inadequate to represent mutualisms, as "they tend to lead to silly solutions in which both populations undergo unbounded exponential growth, in an orgy of mutual benefaction".

To overcome these limitations, and recognizing that mutualisms involve both costs and benefits, such associations between species have begun to be thought as consumer-resource interactions, not unlike predator-prey interactions, but in which benefits outweigh costs (Holland and DeAngelis [13]). In this unifying framework, most mutualisms fit one of the following categories: two-way consumer-resource interactions, one-way consumer-resource interactions and indirect mutualisms via a third species consumer or resource, and also one of the six food web topologies given in [13]. Under these assumptions, saturating functions for resource supply and costs associated to providing resources act as limiting factors, preventing unbounded growth.

In Vargas-De-León [24], global stability conditions for two-species models of mutualism are investigated by using suitably constructed Lyapunov functionals and LaSalle's invariance principle. The models of concern in [24] are

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

introduced by Vandermeer and Boucher in [23] to investigate the situation in which the effects of mutualism are density independent and

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

introduced by Wolin and Lawlor in [27] to represent the situation in which the mutualism has the most impact at higher densities. In the above models, both representing facultative mutualisms, r_i is the intrinsic birth rate of species x_i, while K_i and e_i are 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 quantifying the mutualistic support the species give to each other. Both models were initially introduced without accounting for the effects of harvesting. Also, if one species is missing, the other behaves in the same way in both models, namely in a logistic fashion.

In Georgescu and Zhang [7], paper which attempts to obtain global stability results for mutualisms under more general conditions than those of [24], a general model of a mutualistic interaction is considered:

$$\begin{aligned} \frac{dx_1}{dt} &= a_1(x_1) + f_1(x_1)g_1(x_2) \\ \frac{dx_2}{dt} &= a_2(x_2) + f_2(x_2)g_2(x_1). \end{aligned} \tag{3}$$

Several sets of hypotheses involving in various proportions monotonicity properties and sign conditions are imposed upon the real continuous functions a_1, a_2, f_1, f_2, g_1, g_2, assuming *a priori* the existence of a coexisting equilibrium $\mathbf{E}^* = (x_1^*, x_2^*)$. Global stability properties for $\mathbf{E}^*$ under the above-mentioned sets of hypotheses are obtained with the help of the following Lyapunov functionals:

$$\begin{aligned} V_1(x_1, x_2) &= \int_{x_1^*}^{x_1} \frac{g_2(\theta) - g_2(x_1^*)}{f_1(\theta)} d\theta + \int_{x_2^*}^{x_2} \frac{g_1(\theta) - g_1(x_2^*)}{f_2(\theta)} d\theta, \\ V_2(x_1, x_2) &= \int_{x_1^*}^{x_1} \left(1 - \frac{g_2(\theta)}{g_2(x_1^*)}\right) \frac{1}{a_1(\theta)} d\theta + \int_{x_2^*}^{x_2} \left(1 - \frac{g_1(\theta)}{g_1(x_2^*)}\right) \frac{1}{a_2(\theta)} d\theta, \\ V_3(x_1, x_2) &= \int_{x_1^*}^{x_1} \left(1 - \frac{g_2(x_1^*)}{g_2(\theta)}\right) \frac{1}{f_1(\theta)} d\theta \\ &\quad + \left[\int_{x_2^*}^{x_2} \left(1 - \frac{g_1(x_2^*)}{g_1(\theta)}\right) \frac{1}{f_2(\theta)} d\theta\right] \frac{g_1(x_2^*)}{g_2(x_1^*)}. \end{aligned}$$

The functional V_1, in fact a generalization of the classical Lotka-Volterra logarithmic functional, was first introduced in Harrison [10], although with different signs of the numerators, due to the fact that the interaction considered in [10] is a predation, not a mutualism. See Korobeinikov [16] and Georgescu *et al.* [5] for the use of functionals related to V_3 to establish the stability of general predator-prey models, Goh [8], Vargas-De-León and Gómez-Alcaraz [26] for stability results for models of mutualism or commensalism by a related approach. See also Korobeinikov [14, 15], Georgescu and Hsieh [4], Georgescu and Zhang [6], Vargas-De-León [25], Melnik and Korobeinikov [19], McCluskey [18] for results on the stability of disease propagation models via related functionals. Note that [25] and [6] allow for the possibility of relapse, while [19] allows for age structure and [18] allows for varying infectivity.

However, a number of assumptions in [7], although having a certain degree of generality, are rather involved and tailored to the particularities of the models in [24], which they attempt to enlarge. The main results in [7] are given in four theorems. Two of them require strong monotonicity conditions on the components of (3) such as:

$$\frac{a_1}{f_1} + g_2 \text{ and } \frac{a_2}{f_2} + g_1 \text{ decreasing,} \tag{4}$$

or

$$\frac{f_1}{a_1} + \frac{1}{g_2} \text{ and } \frac{f_2}{a_2} + \frac{1}{g_1} \text{ increasing if } g_1 g_2 > 0 \text{ and decreasing otherwise.} \tag{5}$$

This last condition is used together with sign conditions on these functions:

$$a_2 g_1 < 0 \text{ and } a_1 g_2 < 0 \text{ on } (0, \infty).$$

The other two theorems use weaker monotonicity conditions but the trade-off is that they each require two extra inequalities, which are necessary for the use of V_3 and V_1, respectively. These are rather lengthy and involving several auxiliary functions.

Nevertheless, there are biologically relevant situations for which some of these assumptions do not apply. In what follows, we shall prove that the Lyapunov functionals V_1, V_2, V_3 are also useful for the study of other models of mutualism, namely for a model with restricted growth rates proposed by Graves *et al.* in [9] and for versions of (1) and (2) featuring a Richards growth function instead of the classical logistic one. As a byproduct, we derive the fact that a self-limiting term of a higher order prevents unbounded growth and promotes global stability.

2. A mutualistic model with restricted growth rates.

In this section, we shall employ the Lyapunov functional V_3 in order to establish the global stability of the coexisting equilibrium for the following model with restricted growth rates

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + c_1 x_1 (1 - e^{-\alpha_2 x_2}) \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + c_2 x_2 (1 - e^{-\alpha_1 x_1}), \end{aligned} \tag{6}$$

proposed by Graves *et al.* in [9]. Named by its proponents "limited per capita growth rate (LGR) mutualism model", the model (6) assumes that each species enhances the growth rate of the other without affecting its carrying capacity. The key assumption made in [9] to derive (6) is that the marginal rate of change for the per capita growth rate of each species due to the increase of the other species is proportional to the difference between the maximum growth rate and the current growth rate. Sufficient biological evidence exists for this modeling assumption such as symbioses between plants and nitrogen-fixing microorganisms (see a detailed description in [9]).

We assume here that r_1, c_1, α_1, r_2, c_2, $\alpha_2 > 0$, that is, the model (6) describes a facultative mutualism (although, *mutatis mutandis*, our approach can accommodate obligate mutualisms as well) and, in the absence of a species, the growth of the other is of a logistic nature. Let us observe first that (6) fits the abstract framework (3), with

$$a_1(x_1) = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right), \quad a_2(x_2) = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right), \quad f_1(x_1) = c_1 x_1,$$
$$g_1(x_2) = 1 - e^{-\alpha_2 x_2}, \quad f_2(x_2) = c_2 x_2, \quad g_2(x_1) = 1 - e^{-\alpha_1 x_1}.$$

A quick review of the assumptions used in [7] shows that none of the stability theorems there can be applied for (6). For example assumption (4) no longer holds. Furthermore, the condition on $a_2 g_1$ and $a_1 g_2$ to be negative on $(0, \infty)$ cannot be satisfied here. This means that the theorem in [7] that uses (5) is also inapplicable. The same is true for the theorems that require the auxiliary inequalities.

By a classical positivity argument for Kolmogorov models of population dynamics, it is seen that $(0, \infty) \times (0, \infty)$ is an invariant region for the system (6). Let us now establish the existence of a coexisting equilibrium for (6).

Theorem 2.1. *The system* (6) *has a unique coexisting equilibrium* $\mathbf{E}^* = (x_1^*, x_2^*)$.

Proof. First, it is seen that the coordinates x_1^*, x_2^* of the coexisting equilibrium $\mathbf{E}^*$ should satisfy the following relations

$$x_1^* = K_1 \left(1 + \frac{c_1}{r_1}\left(1 - e^{-\alpha_2 x_2^*}\right)\right), \quad x_2^* = K_2 \left(1 + \frac{c_2}{r_2}\left(1 - e^{-\alpha_1 x_1^*}\right)\right), \tag{7}$$

which lead to

$$x_1^* - K_1 \left\{1 + \frac{c_1}{r_1}\left[1 - e^{-\alpha_2 K_2 \left(1 + \frac{c_2}{r_2}\left(1 - e^{-\alpha_1 x_1^*}\right)\right)}\right]\right\} = 0. \tag{8}$$

Defining $\varphi : [0, \infty) \to \mathbb{R}$ by

$$\varphi(x) = x - K_1 \left\{1 + \frac{c_1}{r_1}\left[1 - e^{-\alpha_2 K_2 \left(1 + \frac{c_2}{r_2}\left(1 - e^{-\alpha_1 x}\right)\right)}\right]\right\} = 0,$$

one notes that φ is of class C^1 on $[0, \infty)$, $\varphi(0) < 0$, $\lim_{x\to\infty} \varphi(x) = +\infty$ and φ' is strictly increasing on $[0, \infty)$, which establishes the existence and uniqueness of a strictly positive root of (8). Consequently, the system (6) has a unique coexisting equilibrium $\mathbf{E}^* = (x_1^*, x_2^*)$. □

After having proved the existence and uniqueness of the coexisting equilibrium, we are now ready to discuss its stability. The first hurdle is the proper choice of a Lyapunov functional. In our settings, V_2 is unusable, due to the terms $\frac{1}{a_1}$ and $\frac{1}{a_2}$, which will not simplify or be everywhere defined. Also, the line of thought involving V_1, perhaps the simplest of all three Lyapunov functionals, requires a particular inequality between parameters to hold, namely $\alpha_1\alpha_2 \leq \frac{r_1 r_2}{c_1 c_2}$. We are now left with using V_3.

We first note that, in this situation, V_3 takes the following form

$$\begin{aligned} V_3(x_1, x_2) = &\int_{x_1^*}^{x_1} \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 \theta}}{1 - e^{-\alpha_1 \theta}} \frac{1}{c_1 \theta} d\theta \\ &+ \left(\int_{x_2^*}^{x_2} \frac{e^{-\alpha_2 x_2^*} - e^{-\alpha_2 \theta}}{1 - e^{-\alpha_2 \theta}} \frac{1}{c_2 \theta} d\theta\right) \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}}. \end{aligned} \tag{9}$$

Using V_3, we may establish the following global stability result, whose proof is given in Appendix A.

Theorem 2.2. *The coexisting equilibrium* $\mathbf{E}^*$ *is globally asymptotically stable in* $(0, \infty) \times (0, \infty)$.

Formally, it would have been possible to write (6) in the following equivalent form

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left(C_1 - \frac{x_1}{K_1}\right) - c_1 x_1 e^{-\alpha_2 x_2} \\ \frac{dx_2}{dt} &= r_2 x_2 \left(C_2 - \frac{x_2}{K_2}\right) - c_2 x_2 e^{-\alpha_1 x_1}, \end{aligned} \tag{10}$$

with $C_1 = 1 + \frac{c_1}{r_1}$, $C_2 = 1 + \frac{c_2}{r_2}$, which would have led to a simpler expression of V_3. However, in this equivalent form, g_1 and g_2 have negative signs, while V_3 is constructed for positive g_1 and g_2, requirement which (6) does fulfill, but (10) does not. Also, the monotonicity of the functions defined in (19) is lost using this equivalent form. Actually, this seemingly simpler form fails to meet the conditions for the use of any of the three functionals V_1, V_2, V_3.

3. Mutualistic models with generalized logistic growth.

A modification of the classical logistic (or Verhulst-Pearl) equation, in the form

$$\frac{dx}{dt} = rx\left[1 - \left(\frac{x}{K}\right)^p\right]$$

has been proposed by Richards [22] in 1959 in order to better fit the growth of certain biological populations. In the above, $x = x(t)$ represents the size of the population at time t, r is the intrinsic growth rate of the population, K is its carrying capacity and p is an additional parameter which allows for further flexibility in the formulation of the model, specifically for the proper placement of the inflection point (the point where the growth rate is maximal). Apart from its initial purpose, Richards equation has been found useful, among other uses, to predict the severity of a disease outbreak (Hsieh [11]), for which the inflection point represents the turning point of the outbreak and the growth of the basal area of trees (Pienaar and Turnbull [21]).

We now attempt to treat versions of (1) and (2) featuring generalized logistic (Richards) growth, namely models

$$\begin{aligned}\frac{dx_1}{dt} &= r_1x_1\left[A_1 - \left(\frac{x_1}{K_1}\right)^p\right] + \frac{r_1b_{12}}{K_1}x_1x_2 \\ \frac{dx_2}{dt} &= r_2x_2\left[A_2 - \left(\frac{x_2}{K_2}\right)^p\right] + \frac{r_2b_{21}}{K_2}x_1x_2,\end{aligned} \tag{11}$$

and respectively

$$\begin{aligned}\frac{dx_1}{dt} &= r_1x_1A_1 - \frac{r_1x_1^{p+1}}{K_1^p + b_{12}x_2} \\ \frac{dx_2}{dt} &= r_2x_2A_2 - \frac{r_2x_2^{p+1}}{K_2^p + b_{21}x_1},\end{aligned} \tag{12}$$

with $A_1 = 1 - \frac{e_1}{r_1}$, $A_2 = 1 - \frac{e_2}{r_2}$, $p \geq 1$. Let us assume that $0 \leq e_1 < r_1$, $0 \leq e_2 < r_2$ and that $b_{12}, b_{21} > 0$, $K_1, K_2 > 0$, observing that for $p = 1$ the models (11) and (12) reduce to (1) and (2), respectively. For the sake of a better correspondence with the abstract framework (3), we shall denote the coordinates of the positive equilibria for (11) and (12) with x_1^* and x_2^* as well, since it will always be clear from the context which model (and therefore which equilibrium) is of concern.

As with the model from the previous section, notice that condition (4) no longer applies. For example, for model (11), with $a_1(x_1) = r_1x_1\left[A_1 - \left(\frac{x_1}{K_1}\right)^p\right]$, $f_1(x_1) = r_1x_1$ and $g_2(x_1) = \frac{b_{21}}{K_2}x_1$ we can see that $\frac{a_1}{f_1} + g_2$ is not decreasing for $p > 1$. A similar argument can be made about (12). Denoting $a_1(x_1) = r_1A_1x_1$, $f_1(x_1) = r_1x_1^{p+1}$ and $g_2(x_1) = -\frac{1}{K_2^p + b_{21}x_1}$ we can see that $\frac{a_1}{f_1} + g_2$ is not decreasing on its domain if $p > 1$. In this last case, condition (5) is also not satisfied.

Let us concentrate on the model (11) first. We start with proving the existence of the coexisting equilibrium of (11), the proof being parallel to that of Theorem 2.1.

Theorem 3.1. *If $p = 1$, then the system (11) has a unique coexisting equilibrium $\mathbf{E_1^*} = (x_1^*, x_2^*)$ if and only if $b_{12}b_{21} < 1$. If $p > 1$, then the system (11) has a unique coexisting equilibrium $\mathbf{E_1^*} = (x_1^*, x_2^*)$ regardless of the value of $b_{12}b_{21}$.*

Proof. As seen from (11), the coordinates x_1^*, x_2^* of the positive equilibrium $\mathbf{E_1^*}$ should satisfy the following relations

$$A_1 - \left(\frac{x_1^*}{K_1}\right)^p + \frac{b_{12}x_2^*}{K_1} = 0, \quad A_2 - \left(\frac{x_2^*}{K_2}\right)^p + \frac{b_{21}x_1^*}{K_2} = 0 \tag{13}$$

which altogether lead to the equation

$$A_2 - \left(\frac{x_2^*}{K_2}\right)^p + b_{21}\frac{K_1}{K_2}\left(A_1 + \frac{b_{12}x_2^*}{K_1}\right)^{\frac{1}{p}} = 0. \tag{14}$$

For $p = 1$, it is seen that (14) reduces to

$$A_2 - \frac{x_2^*}{K_2} + b_{21}\frac{K_1}{K_2}\left(A_1 + \frac{b_{12}x_2^*}{K_1}\right) = 0,$$

which has a positive solution $x_2^* = \frac{A_2K_2 + b_{21}A_1K_1}{1 - b_{12}b_{21}}$ if and only if $b_{12}b_{21} < 1$. In this circumstance, x_1^* is also uniquely defined by $x_1^* = \frac{A_1K_1 + b_{12}A_2K_2}{1 - b_{12}b_{21}}$.

Let us now suppose that $p > 1$ and define $\varphi_1 : [0, \infty) \to \mathbb{R}$ by

$$\varphi_1(x) = A_2 - \left(\frac{x}{K_2}\right)^p + b_{21}\frac{K_1}{K_2}\left(A_1 + \frac{b_{12}x}{K_1}\right)^{\frac{1}{p}}.$$

One notes that φ_1 is of class C^1 on $[0, \infty)$, $\varphi_1(0) > 0$, $\lim_{x\to\infty} \varphi_1(x) = -\infty$, since $p > 1 > \frac{1}{p}$, and φ_1' is strictly decreasing on $[0, \infty)$, which establishes the existence and uniqueness of a strictly positive root of (14). Consequently, the system (11) has a unique coexisting equilibrium $\mathbf{E_1^*} = (x_1^*, x_2^*)$ whose coordinates verify the equilibrium relations (13). □

The fact that no further existence condition is required for $p > 1$ does not come as a surprise. If $p = 1$, the model (11) actually represents a Lotka-Volterra mutualism, which is still prone to exponential growth, since the mutualistic terms $\frac{r_1b_{12}}{K_1}x_1x_2$ and $\frac{r_2b_{21}}{K_2}x_1x_2$ are of order 2 with respect to (x_1, x_2), the same as the self-limiting terms $\frac{r_1}{K_1}x_1^2$ and $\frac{r_2}{K_2}x_2^2$. Consequently, a condition limiting the combined strength of the mutualistic interactions is needed in order to prevent unrestricted growth. If $p > 1$, however, the self-limiting terms are of a higher order, $p + 1$, than the mutualistic terms, which remain of order 2, and no further precaution is needed.

To prove the global stability of $\mathbf{E_1^*}$, let us first note that

$$\left(1 - \frac{1}{x}\right)(1 - x^p) \leq 0, \qquad \text{for } x > 0, \quad p \geq 0, \tag{15}$$

inequality which is of great importance in what follows. Note also that if $p = 0$, the left-hand side is identically 0, while if $p > 0$ the equality holds if and only if $x = 1$.

Let us observe that (11) fits the abstract framework (3), with

$$a_1(x_1) = r_1x_1\left[A_1 - \left(\frac{x_1}{K_1}\right)^p\right], \quad a_2(x_2) = r_2x_2\left[A_2 - \left(\frac{x_2}{K_2}\right)^p\right],$$

$$f_1(x_1) = x_1, \quad g_1(x_2) = \frac{r_1b_{12}x_2}{K_1}, \quad f_2(x_2) = x_2, \quad g_2(x_1) = \frac{r_2b_{21}x_1}{K_2}.$$

In this situation, V_3 takes the form

$$\begin{aligned} V_3(x_1,x_2) &= \int_{x_1^*}^{x_1}\left(1-\frac{x_1^*}{\theta}\right)\frac{1}{\theta}d\theta + \frac{r_1 b_{12} K_2 x_2^*}{r_2 b_{21} K_1 x_1^*}\left[\int_{x_2^*}^{x_2}\left(1-\frac{x_2^*}{\theta}\right)\frac{1}{\theta}d\theta\right] \\ &= \left(\ln\frac{x_1}{x_1^*}+\frac{x_1^*}{x_1}-1\right)+\frac{r_1 b_{12} K_2 x_2^*}{r_2 b_{21} K_1 x_1^*}\left(\ln\frac{x_2}{x_2^*}+\frac{x_2^*}{x_2}-1\right). \end{aligned}$$

Using again V_3, we may establish the following global stability result, whose proof is given in Appendix B.

Theorem 3.2. *The coexisting equilibrium* $\mathbf{E_1^*}$ *is globally asymptotically stable in* $(0,\infty)\times(0,\infty)$.

Let us now turn our attention to the study of the model (12). Although the mutualistic interaction acts now in a different way, by decreasing the death rate of each species, rather than increasing the birth rate, as it previously did, one would again expect a conclusion similar to the one obtained for (11) by comparing the orders of magnitude of positive and negative terms in each right-hand side. Namely, if $p = 1$, the positive and negative terms have equal order and a further condition is needed to prevent exponential growth. If $p > 1$, the negative terms have a larger order and succeed in limiting the growth of the solutions on their own.

The existence of the coexisting equilibrium can be proved via an argument similar to the one employed for the proof of Theorem 3.1. One then obtains the following result.

Theorem 3.3. *If* $p = 1$*, then the system* (12) *has a unique coexisting equilibrium* $\mathbf{E_2^*} = (x_1^*, x_2^*)$ *if and only if* $A_1A_2b_{12}b_{21} < 1$*. If* $p > 1$*, then the system* (12) *has a unique coexisting equilibrium* $\mathbf{E_2^*} = (x_1^*, x_2^*)$ *regardless of the value of* $A_1A_2b_{12}b_{21}$.

Let us also observe that (12) fits the abstract framework (3), with

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

In this situation, having in view that

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

V_1 takes the form

$$\begin{aligned} V_1(x_1,x_2) &= \frac{A_2 b_{21}}{(x_2^*)^p r_1}\int_{x_1^*}^{x_1}\frac{\theta - x_1^*}{(K_2^p + b_{21}\theta)\theta^{p+1}}d\theta \\ &\quad + \frac{A_1 b_{12}}{(x_1^*)^p r_2}\int_{x_2^*}^{x_2}\frac{\theta - x_2^*}{(K_1^p + b_{12}\theta)\theta^{p+1}}d\theta. \end{aligned}$$

Using V_1 this time (or, alternatively, V_2), one may obtain the following global stability result, whose proof is given in Appendix C.

Theorem 3.4. *The coexisting equilibrium* $\mathbf{E_2^*}$ *is globally asymptotically stable in* $(0,\infty)\times(0,\infty)$.

It is to be noted that our Lyapunov functionals can be employed to discuss the stability of certain models of commensalism such as those treated in Vargas-De-León and Gómez-Alcaraz [26], although not without precautions, since, depending on the choices of f_1, f_2, g_1, g_2, several denominators of V_1, V_2, V_3 are null, precluding the respective functional from further use. Also, even after a proper choice of functional, the x_1-part or the x_2-part of such functional is null, depending upon which species is not influenced by the other, and should be replaced with a term defined *ad hoc*.

4. Conclusions.

Establishing global stability of equilibria in biological models is never a trivial undertaking from a mathematical perspective. Nevertheless, it is highly valuable whenever it is achievable. Most authors rely on local stability theorems for which linearization provides an algorithm that can be applied in all cases (although computational difficulties may arise even in this case). Local stability results do not usually provide a direct information on the basin of attraction of the locally stable equilibrium. From a biological perspective, this is significant because the model is a crude approximation of reality and, if the basin of attraction is small, then a question arises whether the modeled population can realistically be imagined as starting in that basin of attraction to further conclude the convergence toward the equilibrium.

While no universally suitable Lyapunov function exists for all models, we have seen that several types of functions proved suitable for this role. The functionals V_1, V_2 and V_3 described at the beginning of this paper were used in several cases, including in [7] that provides a general mutualistic model. In that generalization, several technical assumptions were inevitable. However, important biological features do not fit the framework of these assumptions (while other certainly do). In this paper we showed that the functionals mentioned before can be used in several other models of mutualsim that do not satisfy all of the assumptions in [7], namely mutualistic models with restricted growth rate and generalized logistic growth. As mentioned before in this paper, both of these models are important from a biological perspective due to either field evidence and/or added realism by avoiding exponential population growth. Thus, our main result consists in expanding the area of usefulness of these functionals in establishing stability results for these types of models.

This is by no means exhaustive. There are still many more possible models of mutualism or commensalism that do not fit all of the assumptions described in [7] or in the present paper. Some examples are Allee effects for the part of the model that describes the independent growth rate of each species or more complex functional forms for the interaction part between the two. Incorporating these assumptions will open research questions not only concerning stability results but also interesting biological ones such as: under what conditions mutualistic or commensalistic species can avoid or lower the Allee threshold which is an interesting question to ask regarding endangered species. This research is currently underway and we will report it in a future article.

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Appendix A. Proof of Theorem 2.2.

Proof. First, it is seen that V_3 increases whenever any of $|x_1 - x_1^*|$ and $|x_2 - x_2^*|$ increases and that $V_3(x_1, x_2) \geq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. Also, the level sets of V_3 do not have limit points on the boundary of $(0, \infty) \times (0, \infty)$ since $V_3(x_1, x_2)$ tends to ∞ if either x_1 or x_2 tends to 0 or to ∞.

We now evaluate the derivative of V_3 along the solutions of (6). Our approach is to split $\dot{V_3}$ into two categories of terms, namely terms that can be evaluated by means of monotonicity of certain auxiliary functions Φ_1 and Φ_2 to be introduced below and terms that can be evaluated by means of AM–GM inequality. To this purpose, two equilibrium conditions derived from (7) will be of great importance. One sees that

$$\begin{aligned}
\dot{V_3} &= \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \frac{1}{c_1 x_1} \frac{dx_1}{dt} + \frac{e^{-\alpha_2 x_2^*} - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2}} \frac{1}{c_2 x_2} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \frac{dx_2}{dt} \\
&= \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \frac{r_1}{c_1} \left[1 - \frac{x_1}{K_1} + \frac{c_1}{r_1}(1 - e^{-\alpha_2 x_2})\right] \\
&\quad + \frac{e^{-\alpha_2 x_2^*} - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2}} \frac{r_2}{c_2} \left[1 - \frac{x_2}{K_2} + \frac{c_2}{r_2}(1 - e^{-\alpha_1 x_1})\right] \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \\
&= T_1 + T_2.
\end{aligned} \tag{16}$$

Let us observe that, by algebraic manipulations

$$\begin{aligned}
T_1 &= \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \frac{r_1}{c_1} \\
&\quad \cdot \left[\frac{e^{-\alpha_1 x_1} - e^{-\alpha_1 x_1^*}}{1 - e^{-\alpha_1 x_1^*}} + \frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1^*}} - \frac{x_1}{K_1} + \frac{c_1}{r_1}(1 - e^{-\alpha_2 x_2})\right] \\
&= \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \frac{r_1}{c_1} \frac{e^{-\alpha_1 x_1} - e^{-\alpha_1 x_1^*}}{1 - e^{-\alpha_1 x_1^*}} \\
&\quad + \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \left[\frac{r_1}{c_1}\left(\frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1^*}} - \frac{x_1}{K_1}\right) + 1 - e^{-\alpha_2 x_2}\right] \\
&= T_{11} + T_{12}.
\end{aligned} \tag{17}$$

Note that $T_{11} \leq 0$, with equality if and only if $x_1 = x_1^*$. Also, from the equilibrium relations (7), it follows that

$$1 = \frac{x_1^*}{K_1} - \frac{c_1}{r_1}\left(1 - e^{-\alpha_2 x_2^*}\right). \tag{18}$$

Consequently, by substituting (18) into (17),

$$\begin{aligned}
T_{12} &= \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \left[\frac{r_1}{c_1} \frac{x_1}{K_1} \left(\frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1^*}} \frac{K_1}{x_1} - 1\right) + 1 - e^{-\alpha_2 x_2}\right] \\
&= \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \\
&\quad \cdot \left\{\frac{r_1}{c_1} \frac{x_1}{K_1} \left[\frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1^*}} \frac{K_1}{x_1} \left(\frac{x_1^*}{K_1} - \frac{c_1}{r_1}\left(1 - e^{-\alpha_2 x_2^*}\right)\right) - 1\right] + 1 - e^{-\alpha_2 x_2}\right\}
\end{aligned}$$

$$\begin{aligned}
&= \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \\
&\quad \cdot \left\{ \frac{r_1}{c_1} \frac{x_1}{K_1} \left[\frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1^*}} \frac{x_1^*}{x_1} - 1 \right] - \frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1^*}} \left(1 - e^{-\alpha_2 x_2^*} \right) + 1 - e^{-\alpha_2 x_2} \right\}.
\end{aligned}$$

Let us now define

$$\begin{aligned}
\Phi_1 &: (0,\infty) \to (0,\infty), \quad \Phi_1(x) = \frac{1 - e^{-\alpha_1 x}}{x}, \\
\Phi_2 &: (0,\infty) \to (0,\infty), \quad \Phi_2(x) = \frac{1 - e^{-\alpha_2 x}}{x}.
\end{aligned} \tag{19}$$

Noting that

$$\begin{aligned}
\Phi_1'(x) &= -\frac{e^{-\alpha_1 x}}{x^2} \left(e^{\alpha_1 x} - (1 + \alpha_1 x) \right) < 0, \\
\Phi_2'(x) &= -\frac{e^{-\alpha_2 x}}{x^2} \left(e^{\alpha_2 x} - (1 + \alpha_2 x) \right) < 0
\end{aligned}$$

it follows that Φ_1, Φ_2 are strictly decreasing on $(0,\infty)$. With these notations,

$$\begin{aligned}
T_{12} &= \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \frac{r_1}{c_1} \frac{x_1}{K_1} \left[\frac{\Phi_1(x_1)}{\Phi_1(x_1^*)} - 1 \right] \\
&\quad + \left(e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1} \right) \left(-\frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} + \frac{1 - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_1 x_1}} \right) \\
&= T_{121} + T_{122},
\end{aligned}$$

with $T_{121} \le 0$, the equality holding if and only if $x_1 = x_1^*$, since Φ_1 is strictly decreasing. However, the sign of T_{122} is still undetermined.

By a similar argument, one may evaluate the second term T_2 in the right-hand side of (16) and find that

$$\begin{aligned}
T_2 &= \frac{e^{-\alpha_2 x_2^*} - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2}} \frac{r_2}{c_2} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \frac{e^{-\alpha_2 x_2} - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_2 x_2^*}} \\
&\quad + \frac{e^{-\alpha_2 x_2^*} - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2}} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \left[\frac{r_2}{c_2} \left(\frac{1 - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2^*}} - \frac{x_2}{K_2} \right) + 1 - e^{-\alpha_1 x_1} \right] \\
&= T_{21} + T_{22}.
\end{aligned} \tag{20}$$

Note that $T_{21} \le 0$, with equality if and only if $x_2 = x_2^*$. Also, from the equilibrium relations (7), it follows that

$$1 = \frac{x_2^*}{K_2} - \frac{c_2}{r_2} \left(1 - e^{-\alpha_1 x_1^*} \right). \tag{21}$$

Consequently,

$$\begin{aligned}
T_{22} &= \frac{e^{-\alpha_2 x_2^*} - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2}} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \\
&\quad \left\{ \frac{r_2}{c_2} \frac{x_2}{K_2} \left[\frac{1 - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2^*}} \frac{K_2}{x_2} \left(\frac{x_2^*}{K_2} - \frac{c_2}{r_2} \left(1 - e^{-\alpha_1 x_1^*} \right) \right) - 1 \right] + 1 - e^{-\alpha_1 x_1} \right\} \\
&= \frac{e^{-\alpha_2 x_2^*} - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2}} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \\
&\quad \cdot \left\{ \frac{r_2}{c_2} \frac{x_2}{K_2} \left[\frac{1 - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2^*}} \frac{x_2^*}{x_2} - 1 \right] - \frac{1 - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2^*}} (1 - e^{-\alpha_1 x_1^*}) + 1 - e^{-\alpha_1 x_1} \right\}.
\end{aligned}$$

It follows that

$$\begin{aligned}T_{22} &= \frac{e^{-\alpha_2 x_2^*} - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_2 x_2}} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \frac{r_2}{c_2} \frac{x_2}{K_2} \left[\frac{\Phi_2(x_2)}{\Phi_2(x_2^*)} - 1 \right] \\ &\quad + \left(e^{-\alpha_2 x_2^*} - e^{-\alpha_2 x_2} \right) \left(-1 + \frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_2 x_2}} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \right) \\ &= T_{221} + T_{222},\end{aligned}$$

with $T_{221} \leq 0$, the equality holding if and only if $x_2 = x_2^*$, since Φ_2 is strictly decreasing. Again, the sign of T_{222} is undetermined.

By using (16), (17) and (20), it now follows that

$$\begin{aligned}\dot{V}_3 &= T_{11} + T_{121} + T_{21} + T_{221} \\ &\quad + \left(e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1} \right) \left(-\frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} + \frac{1 - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_1 x_1}} \right) \\ &\quad + \left(e^{-\alpha_2 x_2^*} - e^{-\alpha_2 x_2} \right) \left(-1 + \frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_2 x_2}} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \right) \\ &= T_{11} + T_{121} + T_{21} + T_{221} \\ &\quad + \left(-1 + e^{-\alpha_1 x_1^*} + 1 - e^{-\alpha_1 x_1} \right) \left(-\frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} + \frac{1 - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_1 x_1}} \right) \\ &\quad + \left(-1 + e^{-\alpha_2 x_2^*} + 1 - e^{-\alpha_2 x_2} \right) \left(-1 + \frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_2 x_2}} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \right) \\ &= T_{11} + T_{121} + T_{21} + T_{221} \\ &\quad + \left(1 - e^{-\alpha_2 x_2^*} \right) \left[2 - \frac{1 - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_1 x_1}} \frac{1 - e^{-\alpha_1 x_1^*}}{1 - e^{-\alpha_2 x_2^*}} - \frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_2 x_2}} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \right].\end{aligned}$$

Note that

$$2 - \frac{1 - e^{-\alpha_2 x_2}}{1 - e^{-\alpha_1 x_1}} \frac{1 - e^{-\alpha_1 x_1^*}}{1 - e^{-\alpha_2 x_2^*}} - \frac{1 - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_2 x_2}} \frac{1 - e^{-\alpha_2 x_2^*}}{1 - e^{-\alpha_1 x_1^*}} \leq 0,$$

by AM–GM inequality (i.e. the inequality between the arithmetic mean and the geometric mean for two positive numbers), with equality if and only if $\frac{1-e^{-\alpha_1 x_1}}{1-e^{-\alpha_2 x_2}} = \frac{1-e^{-\alpha_1 x_1^*}}{1-e^{-\alpha_2 x_2^*}}$. Since the previous remarks yield that $T_{11} + T_{121} \leq 0$ with equality if and only if $x_1 = x_1^*$ and $T_{21} + T_{221} \leq 0$ with equality if and only if $x_2 = x_2^*$, we have $\dot{V}_3 \leq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. Since $\mathbf{E}^*$ is the only invariant set in $M = \left\{ (x_1, x_2); \dot{V}_3(x_1, x_2) = 0 \right\}$, then, by LaSalle's invariance theorem, $\mathbf{E}^*$ is globally asymptotically stable in $(0, \infty) \times (0, \infty)$. □

Appendix B. Proof of Theorem 3.2.

Proof. First, it is seen that V_3 increases whenever any of $|x_1 - x_1^*|$ and $|x_2 - x_2^*|$ increases and that $V_3(x_1, x_2) \geq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. Also, the level sets of V_3 do not have limit points on the boundary of $(0, \infty) \times (0, \infty)$ since $V_3(x_1, x_2)$ tends to ∞ if either x_1 or x_2 tends to 0 or to ∞.

We now evaluate the derivative of V_3 along the solutions of (11). We shall split $\dot{V}_3$ into terms that can be estimated by means of (15) and terms that can be estimated by means of AM–GM inequality. To this purpose, we shall also use equilibrium conditions derived from (13). One sees that

$$\begin{aligned}\dot{V}_3 &= \left(\frac{1}{x_1} - \frac{x_1^*}{x_1^2}\right)\frac{dx_1}{dt} + \frac{r_1 b_{12} K_2 x_2^*}{r_2 b_{21} K_1 x_1^*}\left(\frac{1}{x_2} - \frac{x_2^*}{x_2^2}\right)\frac{dx_2}{dt} \qquad (22)\\ &= r_1\left(1 - \frac{x_1^*}{x_1}\right)\left[A_1 - \left(\frac{x_1}{K_1}\right)^p + \frac{b_{12}x_2}{K_1}\right]\\ &\quad + \frac{r_1 b_{12} K_2 x_2^*}{b_{21} K_1 x_1^*}\left(1 - \frac{x_2^*}{x_2}\right)\left[A_2 - \left(\frac{x_2}{K_2}\right)^p + \frac{b_{21}x_1}{K_2}\right].\end{aligned}$$

We note that the equilibrium conditions (13) imply that

$$\left(A_1 + \frac{b_{12}x_2^*}{K_1}\right)\left(\frac{K_1}{x_1^*}\right)^p = 1; \qquad \left(A_2 + \frac{b_{21}x_1^*}{K_2}\right)\left(\frac{K_2}{x_2^*}\right)^p = 1. \qquad (23)$$

Consequently, by substituting (23) into (22), one obtains by rearranging terms that

$$\begin{aligned}\dot{V}_3 &= r_1\left(1 - \frac{x_1^*}{x_1}\right)\left[A_1 - \left(\frac{x_1}{x_1^*}\right)^p\left(A_1 + \frac{b_{12}x_2^*}{K_1}\right) + \frac{b_{12}x_2}{K_1}\right]\\ &\quad + \frac{r_1 b_{12} K_2 x_2^*}{b_{21} K_1 x_1^*}\left(1 - \frac{x_2^*}{x_2}\right)\left[A_2 - \left(\frac{x_2}{x_2^*}\right)^p\left(A_2 + \frac{b_{21}x_1^*}{K_2}\right) + \frac{b_{21}x_1}{K_2}\right]\\ &= r_1 A_1\left(1 - \frac{x_1^*}{x_1}\right)\left[1 - \left(\frac{x_1}{x_1^*}\right)^p\right]\\ &\quad + r_1 A_2 \frac{b_{12} K_2 x_2^*}{b_{21} K_1 x_1^*}\left(1 - \frac{x_2^*}{x_2}\right)\left[1 - \left(\frac{x_2}{x_2^*}\right)^p\right]\\ &\quad + r_1\left(1 - \frac{x_1^*}{x_1}\right)\frac{b_{12}x_2^*}{K_1}\left[\frac{x_2}{x_2^*} - \left(\frac{x_1}{x_1^*}\right)^p\right]\\ &\quad + \frac{r_1 b_{12} K_2 x_2^*}{b_{21} K_1 x_1^*}\left(1 - \frac{x_2^*}{x_2}\right)\frac{b_{21}x_1^*}{K_2}\left[\frac{x_1}{x_1^*} - \left(\frac{x_2}{x_2^*}\right)^p\right]\\ &= T_1 + T_2 + T_3 + T_4.\end{aligned}$$

By (15), $T_1 \le 0$ and $T_2 \le 0$, with inequality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$, respectively. We now establish the sign of $T_3 + T_4$. It is seen that

$$\begin{aligned}T_3 + T_4 &= r_1\frac{b_{12}x_2^*}{K_1}\left\{\left(1 - \frac{x_1^*}{x_1}\right)\left[\frac{x_2}{x_2^*} - \left(\frac{x_1}{x_1^*}\right)^p\right] + \left(1 - \frac{x_2^*}{x_2}\right)\left[\frac{x_1}{x_1^*} - \left(\frac{x_2}{x_2^*}\right)^p\right]\right\}\\ &= r_1\frac{b_{12}x_2^*}{K_1}\left\{\frac{x_1}{x_1^*}\left(1 - \frac{x_1^*}{x_1}\right)\left[1 - \left(\frac{x_1}{x_1^*}\right)^{p-1}\right]\right.\\ &\qquad \left. + \frac{x_2}{x_2^*}\left(1 - \frac{x_2^*}{x_2}\right)\left[1 - \left(\frac{x_2}{x_2^*}\right)^{p-1}\right] + 2 - \frac{x_1^* x_2}{x_1 x_2^*} - \frac{x_2^* x_1}{x_2 x_1^*}\right\}\\ &\le 0,\end{aligned}$$

since the first two terms inside the square brackets are negative by (15) (this is where restriction $p \ge 1$ comes from), being equal to 0 if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$ (if $p > 1$) and being identically 0 if $p = 1$, while the third one is negative by AM–GM inequality, being equal to 0 if and only if $\frac{x_1}{x_1^*} = \frac{x_2}{x_2^*}$. Since the previous remarks yield that $T_1 \le 0$ with equality if and only if $x_1 = x_1^*$, $T_2 \le 0$ with equality if and only if $x_2 = x_2^*$, and $T_3 + T_4 \le 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$ (if $p > 1$) and if and only if $\frac{x_1}{x_1^*} = \frac{x_2}{x_2^*}$ (if $p = 1$), it follows that $\dot{V}_3 \le 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. Since $\mathbf{E_1^*}$ is the only invariant set in $M = \left\{(x_1, x_2); \dot{V}_3(x_1, x_2) = 0\right\}$, it follows by LaSalle's invariance theorem that $\mathbf{E_1^*}$ is globally asymptotically stable in $(0, \infty) \times (0, \infty)$. □

Appendix C. Proof of Theorem 3.4.

Proof. First, it is seen that V_1 increases whenever any of $|x_1 - x_1^*|$ and $|x_2 - x_2^*|$ increases and that $V_1(x_1, x_2) \geq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. Also, the level sets of V_1 do not have limit points on the boundary of $(0, \infty) \times (0, \infty)$ since $V_1(x_1, x_2)$ tends to ∞ if either x_1 or x_2 tends to 0 or to ∞.

We now evaluate the derivative of V_1 along the solutions of (12). We shall split $\dot{V}_1$ into terms that can be estimated by means of (15) and terms that can be estimated by means of AM–GM inequality. To this purpose, we shall also use reformulations of the equilibrium conditions. One sees that

$$
\begin{aligned}
\dot{V}_1 &= \frac{A_2 b_{21}}{(x_2^*)^p r_1} \frac{x_1 - x_1^*}{(K_2^p + b_{21} x_1) x_1^{p+1}} \frac{dx_1}{dt} + \frac{A_1 b_{12}}{(x_1^*)^p r_2} \frac{x_2 - x_2^*}{(K_1^p + b_{12} x_2) x_2^{p+1}} \frac{dx_2}{dt} \\
&= \frac{A_2 b_{21}}{(x_2^*)^p} \frac{1}{(K_2^p + b_{21} x_1)(K_1^p + b_{12} x_2)} \frac{x_1 - x_1^*}{x_1^p} \left[A_1 (K_1^p + b_{12} x_2) - x_1^p\right] \\
&\quad + \frac{A_1 b_{12}}{(x_1^*)^p} \frac{1}{(K_2^p + b_{21} x_1)(K_1^p + b_{12} x_2)} \frac{x_2 - x_2^*}{x_2^p} \left[A_2 (K_2^p + b_{21} x_1) - x_2^p\right].
\end{aligned}
\tag{24}
$$

Note that the equilibrium relations imply that

$$
A_1 \frac{K_1^p + b_{12} x_2^*}{(x_1^*)^p} = 1, \quad A_2 \frac{K_2^p + b_{21} x_1^*}{(x_2^*)^p} = 1. \tag{25}
$$

Consequently, by substituting (25) into (24), one may obtain by rearranging terms that

$$
\begin{aligned}
\dot{V}_1 = &\frac{A_2 b_{21}}{(x_2^*)^p} \frac{1}{(K_2^p + b_{21} x_1)(K_1^p + b_{12} x_2)} \frac{x_1 - x_1^*}{x_1^p} \\
&\quad \cdot \left[A_1 (K_1^p + b_{12} x_2) - x_1^p A_1 \frac{K_1^p + b_{12} x_2^*}{(x_1^*)^p}\right] \\
&+ \frac{A_1 b_{12}}{(x_1^*)^p} \frac{1}{(K_2^p + b_{21} x_1)(K_1^p + b_{12} x_2)} \frac{x_2 - x_2^*}{x_2^p} \\
&\quad \cdot \left[A_2 (K_2^p + b_{21} x_1) - x_2^p A_2 \frac{K_2^p + b_{21} x_1^*}{(x_2^*)^p}\right] \\
= &\frac{A_2 b_{21}}{(x_2^*)^p} \frac{1}{(K_2^p + b_{21} x_1)(K_1^p + b_{12} x_2)} \frac{1}{x_1^{p-1}} \left(1 - \frac{x_1^*}{x_1}\right) A_1 K_1^p \left[1 - \left(\frac{x_1}{x_1^*}\right)^p\right] \\
&+ \frac{A_1 b_{12}}{(x_1^*)^p} \frac{1}{(K_2^p + b_{21} x_1)(K_1^p + b_{12} x_2)} \frac{1}{x_2^{p-1}} \left(1 - \frac{x_2^*}{x_2}\right) A_2 K_2^p \left[1 - \left(\frac{x_2}{x_2^*}\right)^p\right] \\
&+ \frac{A_2 b_{21} A_1 b_{12}}{(K_2^p + b_{21} x_1)(K_1^p + b_{12} x_2)} \frac{x_1 - x_1^*}{x_1^p} \frac{1}{(x_2^*)^{p-1}} \left[\frac{x_2}{x_2^*} - \left(\frac{x_1}{x_1^*}\right)^p\right] \\
&+ \frac{A_2 b_{21} A_1 b_{12}}{(K_2^p + b_{21} x_1)(K_1^p + b_{12} x_2)} \frac{x_2 - x_2^*}{x_2^p} \frac{1}{(x_1^*)^{p-1}} \left[\frac{x_1}{x_1^*} - \left(\frac{x_2}{x_2^*}\right)^p\right] \\
= &T_1 + T_2 + T_3 + T_4.
\end{aligned}
$$

By (15), $T_1 \leq 0$ and $T_2 \leq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$, respectively. We note also that

$$T_3 + T_4 = \frac{A_2 b_{21} A_1 b_{12}}{(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)} \frac{1}{(x_1^* x_2^*)^{p-1}} E,$$

with

$$\begin{aligned} E &= \left(1 - \frac{x_1^*}{x_1}\right)\left(\frac{x_1^*}{x_1}\right)^{p-1}\left[\frac{x_2}{x_2^*} - \left(\frac{x_1}{x_1^*}\right)^p\right] + \left(1 - \frac{x_2^*}{x_2}\right)\left(\frac{x_2^*}{x_2}\right)^{p-1}\left[\frac{x_1}{x_1^*} - \left(\frac{x_2}{x_2^*}\right)^p\right] \\ &= \frac{x_2}{x_2^*}\left(1 - \frac{x_1^*}{x_1}\right)\left[\left(\frac{x_1^*}{x_1}\right)^{p-1} - 1\right] + \frac{x_1}{x_1^*}\left(1 - \frac{x_2^*}{x_2}\right)\left[\left(\frac{x_2^*}{x_2}\right)^{p-1} - 1\right] \\ &\quad + 2 - \frac{x_2 x_1^*}{x_2^* x_1} - \frac{x_1 x_2^*}{x_1^* x_2} \\ &= \frac{x_2}{x_2^*}\left(\frac{x_1^*}{x_1}\right)^{p-1}\left(1 - \frac{x_1^*}{x_1}\right)\left[1 - \left(\frac{x_1}{x_1^*}\right)^{p-1}\right] \\ &\quad + \frac{x_1}{x_1^*}\left(\frac{x_2^*}{x_2}\right)^{p-1}\left(1 - \frac{x_2^*}{x_2}\right)\left[1 - \left(\frac{x_2}{x_2^*}\right)^{p-1}\right] + 2 - \frac{x_2 x_1^*}{x_2^* x_1} - \frac{x_1 x_2^*}{x_1^* x_2} \\ &\leq 0, \end{aligned}$$

since the first two terms are negative by (15), while the third one is negative by AM–GM inequality. It then follows that $T_3 + T_4 \leq 0$, and consequently $\dot{V}_1 \leq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. Since $\mathbf{E_2^*}$ 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 theorem that $\mathbf{E_2^*}$ is globally asymptotically stable in $(0, \infty) \times (0, \infty)$. $\square$

We shall now observe that a similar conclusion can be reached by using V_2 instead of V_1. To this purpose, let us note that in this situation V_2 is given by

$$V_2(x_1, x_2) = \frac{b_{21}}{r_1 A_1}\int_{x_1^*}^{x_1} \frac{\theta - x_1^*}{(K_2^p + b_{21}\theta)\theta} d\theta + \frac{b_{12}}{r_2 A_2}\int_{x_2^*}^{x_2} \frac{\theta - x_2^*}{(K_1^p + b_{12}\theta)\theta} d\theta.$$

The evalution of the derivative of V_2 along the solutions of (12) gives

$$\begin{aligned} \dot{V}_2 &= \frac{b_{21}}{r_1 A_1}\frac{x_1 - x_1^*}{(K_2^p + b_{21}x_1)x_1}\frac{dx_1}{dt} + \frac{b_{12}}{r_2 A_2}\frac{x_2 - x_2^*}{(K_1^p + b_{12}x_2)x_2}\frac{dx_2}{dt} \\ &= \frac{b_{21}(x_1 - x_1^*)}{A_1(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)}\left[A_1(K_1^p + b_{12}x_2) - x_1^p\right] \\ &\quad + \frac{b_{12}(x_2 - x_2^*)}{A_2(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)}\left[A_2(K_2^p + b_{21}x_1) - x_2^p\right]. \end{aligned}$$

Using (25), it is seen that

$$\begin{aligned} \dot{V}_2 = &\frac{b_{21}(x_1 - x_1^*)}{A_1(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)}\left[A_1(K_1^p + b_{12}x_2) - x_1^p A_1 \frac{K_1^p + b_{12}x_2^*}{(x_1^*)^p}\right] \\ &+ \frac{b_{12}(x_2 - x_2^*)}{A_2(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)}\left[A_2(K_2^p + b_{21}x_1) - x_2^p A_2 \frac{K_2^p + b_{21}x_1^*}{(x_2^*)^p}\right] \end{aligned}$$

$$\begin{aligned}
&= \frac{b_{21}(x_1 - x_1^*)}{A_1(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)} \\
&\qquad \cdot \left\{ K_1^p A_1 \left[1 - \left(\frac{x_1}{x_1^*} \right)^p \right] + A_1 b_{12} \left[x_2 - x_2^* \left(\frac{x_1}{x_1^*} \right)^p \right] \right\} \\
&\quad + \frac{b_{12}(x_2 - x_2^*)}{A_2(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)} \\
&\qquad \cdot \left\{ K_2^p A_2 \left[1 - \left(\frac{x_2}{x_2^*} \right)^p \right] + A_2 b_{21} \left[x_1 - x_1^* \left(\frac{x_2}{x_2^*} \right)^p \right] \right\} \\
&= \frac{b_{21}K_1^p x_1}{(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)} \left(1 - \frac{x_1^*}{x_1} \right) \left[1 - \left(\frac{x_1}{x_1^*} \right)^p \right] \\
&\quad + \frac{b_{12}K_2^p x_2}{(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)} \left(1 - \frac{x_2^*}{x_2} \right) \left[1 - \left(\frac{x_2}{x_2^*} \right)^p \right] \\
&\quad + \frac{b_{12}b_{21}x_1^* x_2^*}{(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)} \left(\frac{x_1}{x_1^*} - 1 \right) \left[\frac{x_2}{x_2^*} - \left(\frac{x_1}{x_1^*} \right)^p \right] \\
&\quad + \frac{b_{12}b_{21}x_1^* x_2^*}{(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)} \left(\frac{x_2}{x_2^*} - 1 \right) \left[\frac{x_1}{x_1^*} - \left(\frac{x_2}{x_2^*} \right)^p \right] \\
&= T_1 + T_2 + T_3 + T_4.
\end{aligned}$$

By (15), it is seen that $T_1 \le 0$ and $T_2 \le 0$, with inequality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$, respectively. Also,

$$\begin{aligned}
T_3 + T_4 &= \frac{b_{12}b_{21}x_1^* x_2^*}{(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)} \\
&\quad \cdot \left\{ \left(1 - \frac{x_1^*}{x_1} \right) \left[\frac{x_2}{x_2^*} \frac{x_1}{x_1^*} - \left(\frac{x_1}{x_1^*} \right)^{p+1} \right] + \left(1 - \frac{x_2^*}{x_2} \right) \left[\frac{x_1}{x_1^*} \frac{x_2}{x_2^*} - \left(\frac{x_2}{x_2^*} \right)^{p+1} \right] \right\} \\
&= \frac{b_{12}b_{21}x_1^* x_2^*}{(K_2^p + b_{21}x_1)(K_1^p + b_{12}x_2)} E_1,
\end{aligned}$$

where

$$\begin{aligned}
E_1 &= \frac{x_1}{x_1^*} \left(1 - \frac{x_1^*}{x_1} \right) \left[1 - \left(\frac{x_1}{x_1^*} \right)^p \right] + \frac{x_1}{x_1^*} \left(1 - \frac{x_1^*}{x_1} \right) \left(\frac{x_2}{x_2^*} - 1 \right) \\
&\quad + \frac{x_1}{x_1^*} \left(1 - \frac{x_1^*}{x_1} \right) \left[1 - \left(\frac{x_1}{x_1^*} \right)^p \right] + \frac{x_2}{x_2^*} \left(1 - \frac{x_2^*}{x_2} \right) \left(\frac{x_1}{x_1^*} - 1 \right) \\
&= \left(\frac{x_1}{x_1^*} \right)^2 \left(1 - \frac{x_1^*}{x_1} \right) \left[1 - \left(\frac{x_1}{x_1^*} \right)^{p-1} \right] + \left(\frac{x_2}{x_2^*} \right)^2 \left(1 - \frac{x_2^*}{x_2} \right) \left[1 - \left(\frac{x_2}{x_2^*} \right)^{p-1} \right] \\
&\quad - \left(\frac{x_1}{x_1^*} - \frac{x_2}{x_2^*} \right)^2.
\end{aligned}$$

By (15), it follows that $E_1 \le 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$ (if $p > 1$) and if and only if $\frac{x_1}{x_1^*} = \frac{x_2}{x_2^*}$ (if $p = 1$). Since the previous remarks yield that $T_1 \le 0$ with equality if and only if $x_1 = x_1^*$, $T_2 \le 0$ with equality if and only if $x_2 = x_2^*$, and $T_3 + T_4 \le 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$ (if $p > 1$) and if and only if $\frac{x_1}{x_1^*} = \frac{x_2}{x_2^*}$ (if $p = 1$), it follows that $\dot{V}_2 \le 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. The rest of the argument is similar to the one displayed above, establishing once again the global stability of E_2^*.

REFERENCES

[1] N. Apreutesei, G. Dimitriu and R. Strugariu, An optimal control problem for a two-prey and one-predator model with diffusion, *Comput. Math. Appl.*, **67** (2014), 2127–2143.

[2] J. L. Bronstein, U. Dieckmann and R. Ferrière, Coevolutionary dynamics and the conservation of mutualisms, in *Evolutionary Conservation Biology* (eds. R. Ferrière, U. Dieckmann and D. Couvet), Cambridge University Press, (2004), 305–326.

[3] A. E. Douglas, *The Symbiotic Habit*, Princeton University Press, Princeton, 2010.

[4] P. Georgescu and 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] P. Georgescu, Y.-H. Hsieh and H. Zhang, A Lyapunov functional for a stage-structured predator-prey model with nonlinear predation rate, *Nonlinear Anal.: Real World Appl.*, **11** (2010), 3653–3665.

[6] P. Georgescu and H. Zhang, A Lyapunov functional for a SIRI model with nonlinear incidence of infection and relapse, *Appl. Math. Comput.*, **219** (2013), 8496–8507.

[7] P. Georgescu and H. Zhang, Lyapunov functionals for two-species mutualisms, *Appl. Math. Comput.*, **226** (2014), 754–764.

[8] B. S. Goh, Stability in models of mutualism, *Am. Nat.*, **113** (1979), 261–275.

[9] W. G. Graves, B. Peckham and J. Pastor, A bifurcation analysis of a differential equations model for mutualism, *Bull. Math. Biol.*, **68** (2006), 1851–1872.

[10] G. W. Harrison, Global stability of predator-prey interactions, *J. Math. Biol.*, **8** (1979), 159–171.

[11] Y.-H. Hsieh, Richards model: A simple procedure for real-time prediction of outbreak severity, in *Modeling and Dynamics of Infectious Diseases* (eds. Z. Ma, J. Wu and Y. Zhou), Series in Contemporary Applied Mathematics (CAM), Higher Education Press, **11** (2009), 216–236.

[12] J. N. Holland and J.L. Bronstein, Mutualism, in *Population Dynamics, Vol 3 of Encyclopedia of Ecology* (eds. S.E. Jorgensen and B.D. Fath), Elsevier, (2008), 2485–2491.

[13] J. N. Holland and D. L. DeAngelis, A consumer-resource approach to the density-dependent population dynamics of mutualism, *Ecology*, **91** (2010), 1286–1295.

[14] A. Korobeinikov, Lyapunov functions and global properties for SEIR and SEIS epidemic models, *Math. Med. Biol.*, **21** (2004), 75–83.

[15] A. Korobeinikov, Lyapunov functions and global stability for SIR and SIRS epidemiological models with non-linear transmission, *Bull. Math. Biol.*, **68** (2006), 615–626.

[16] A. Korobeinikov, Stability of ecosystem: Global properties of a general predator-prey model, *Math. Med. Biol.*, **26** (2009), 309–321.

[17] R. M. May, Models of two interacting populations, in *Theoretical Ecology: Principles and Application* (ed. R. M. May), Saunders, (1976), 78–104.

[18] C. C. McCluskey, Global stability for an SEIR epidemiological model with varying infectivity and infinite delay, *Math. Biosci. Eng.*, **6** (2009), 603–610.

[19] A. V. Melnik and A. Korobeinikov, Lyapunov functions and global stability for SIR and SEIR models with age-dependent susceptibility, *Math. Biosci. Eng.*, **10** (2013), 369–378.

[20] T. M. Palmer and A. K. Brody, Mutualism as reciprocal exploitation: African plant-ants defend foliar but not reproductive structures, *Ecology*, **88** (2007), 3004–3011.

[21] L. V. Pienaar and K. J. Turnbull, The Chapman-Richards generalization of von Bertalanffy's growth model for basal area growth and yield in even-aged stands, *Forest Science*, **19** (1973), 2–22.

[22] F. J. Richards, A flexible growth function for empirical use, *J. Exp. Bot.*, **10** (1959), 290–300.

[23] J. Vandermeer and D. Boucher, Varieties of mutualistic interaction in population models, *J. Theor. Biol.*, **74** (1978), 549–558.

[24] C. Vargas-De-León, Lyapunov functions for two-species cooperative systems, *Appl. Math. Comput.*, **219** (2012), 2493–2497.

[25] C. Vargas-De-León, On the global stability of infectious diseases models with relapse, *Abstraction & Application*, **9** (2013), 50–61.

[26] C. Vargas-De-León and G. Gómez-Alcaraz, Global stability in some ecological models of commensalism between two species, *Biomatemática*, **23** (2013), 139–146.

[27] C. Wolin and L. Lawlor, Models of facultative mutualism: Density effects, *Am. Nat.*, **124** (1984), 843–862.

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