International Journal of Biomathematics
Vol. 10, No. 3 (2017) 1750037 (25 pages)

DOI: 10.1142/S1793524517500371

Global stability results for models of commensalism

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Received 11 August 2015
Accepted 30 September 2016
Published 15 November 2016

We analyze the global stability of the coexisting equilibria for several models of commensalism, first by devising a procedure to modify several Lyapunov functionals which were introduced earlier for corresponding models of mutualism, further confirming their usefulness. It is seen that commensalism promotes global stability, in connection with higher-order self-limiting terms which prevent unboundedness. We then use the theory of asymptotically autonomous systems to prove global stability results for models of commensalism which are subject to Allee effects, finding that commensalisms of appropriate strength can overcome the influence of strong Allee effects.

Keywords: Commensalism; global stability; Lyapunov functional; Allee effects; asymptotically autonomous systems.

Mathematics Subject Classification 2010: Primary 92D40, 34D23; Secondary 93D30

1. Introduction

Depending on the beneficial (+), detrimental (–) or neutral (0) effects of two species on each other's ability to survive, grow or reproduce, interspecies interactions range from mutualism (++) to competition (−−) [15]. Among these possible types, the facilitative ones, in which benefits such as higher growth rates, higher reproductive outputs or sheltering from external risk factors are enjoyed by one or both species, are usually categorized as mutualism and commensalism. Mutualism (++) is therefore a specific form of facilitation in which the association is beneficial for both species. Commensalism (+0), on the other hand, describes a situation in which one species benefits from the association, while the other is left unaffected.

An example of commensalism is the interaction between small plants called epiphytes and the tree on which they grow and from which they derive structural support. Since epiphytes extract nutrients from the atmosphere, not from the tree, and also do not harm or otherwise interfere with its growth in any way, there is little data or reason to support any harm or benefit for the tree. Chemical commensalistic associations occur between bacterial species, one bacterium metabolizing a chemical useless to the second bacterium and releasing residual metabolites which are useful as a source of energy for the second bacterium, which is the sole beneficiary of this association. Such interaction occurs between *Acetobacter oxydans*, which produces fructose by oxidizing mannitol and *Saccharomyces carlsbergensis*, which can metabolize fructose, but cannot metabolize mannitol [14].

While a much higher attention has been devoted to antagonistic interactions (competition and predation) than to the facilitative ones, commensalism has received even less attention than mutualism. A common criticism to the concept of commensalism is that while positive or negative effects are usually easily noticeable, it is rather difficult to establish that a species is truly not affected by the interaction with the other, being argued that interactions are more likely to be asymmetric, one species exhibiting a strong positive response, while the other exhibits a weak positive or negative response to the first [20].

It has long been recognized that, due to a variety of biological reasons, a positive correlation between the size of a population and its per capita growth rate, known as the Allee effect, may exist at small densities. Two of the most common causes are the benefits extracted from group defense or cooperation and an increased chance of reproductive success due to easier mate finding [3, 21, 11].

By the nature of the density dependence, the Allee effects can be classified as weak or strong. If the population exhibits a critical population size below of which extinction is guaranteed, then the Allee effect is called strong, while if there is no such critical threshold, then the Allee effect is called weak.

For instance, the classical logistic model

$$x' = rx\left(1 - \frac{x}{K}\right),$$

for which the per capita growth rate is $f(x) = r\left(1 - \frac{x}{K}\right)$, decreasing for all population densities, exhibits no Allee effects. On the contrary, the model

$$x' = rx\left(\frac{x}{A} - 1\right)\left(1 - \frac{x}{K}\right),$$

for which the per capita growth rate is $f(x) = r\left(\frac{x}{A} - 1\right)\left(1 - \frac{x}{K}\right)$, negative for $x \in (0, A)$, but with derivative $f'(x) = -\frac{2x}{AK} + \left(\frac{1}{A} + \frac{1}{K}\right)$, positive for small x, exhibits a strong Allee effect with threshold equal to A. Finally, the model

$$x' = rx^p\left(1 - \frac{x}{K}\right), \quad p > 1,$$

for which the per capita growth rate is $f(x) = rx^{p-1}\big(1 - \frac{x}{K}\big)$, positive for small x, with derivative $f'(x) = rx^{p-2}\big(p - 1 - \frac{px}{K}\big)$, also positive for small x, exhibits a weak Allee effect.

2. Previous Work on Mutualistic Models and Motivation

In [24], the global stability of the positive equilibria for two-species mutualisms has been investigated by means of Lyapunov's second method. The models of interest in [24] are:

$$\begin{aligned} \frac{dx_1}{dt} &= r_1x_1\left[\left(1 - \frac{e_1}{r_1}\right) - \frac{x_1}{K_1}\right] + \frac{r_1b_{12}}{K_1}x_1x_2, \\ \frac{dx_2}{dt} &= r_2x_2\left[\left(1 - \frac{e_2}{r_2}\right) - \frac{x_2}{K_2}\right] + \frac{r_2b_{21}}{K_2}x_1x_2, \end{aligned} \tag{2.1}$$

introduced by Vandermeer and Boucher in [23] and:

$$\begin{aligned} \frac{dx_1}{dt} &= (r_1 - e_1)x_1 - \frac{r_1x_1^2}{K_1 + b_{12}x_2}, \\ \frac{dx_2}{dt} &= (r_2 - e_2)x_2 - \frac{r_2x_2^2}{K_2 + b_{21}x_1}, \end{aligned} \tag{2.2}$$

introduced by Wolin and Lawlor in [27]. In the above models, both representing facultative mutualisms, r_i represents 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.

An abstract model of a mutualistic interaction, in the form:

$$\begin{aligned} \frac{dx_1}{dt} &= a_1(x_1) + f_1(x_1)g_1(x_2), \\ \frac{dx_2}{dt} &= a_2(x_2) + f_2(x_2)g_2(x_1), \end{aligned} \tag{2.3}$$

has been studied by Georgescu and Zhang in [8], the real continuous functions a_1, a_2, f_1, f_2, g_1, g_2 being assumed to satisfy several combinations of monotonicity properties and sign conditions. The existence of a coexisting equilibrium $\mathbf{E}^* = \big(x_1^*, x_2^*\big)$ has been *a priori* assumed in [8], global stability properties for $\mathbf{E}^*$ being then obtained by means of Lyapunov's second method. In [8], use has been made of the following functionals:

$$\begin{aligned}
V_1(x_1,x_2) &= \int_{x_1^*}^{x_1} \frac{g_2(\theta)-g_2(x_1^*)}{f_1(\theta)}d\theta + \int_{x_2^*}^{x_2} \frac{g_1(\theta)-g_1(x_2^*)}{f_2(\theta)}d\theta,\\
V_2(x_1,x_2) &= \int_{x_1^*}^{x_1} \left(1-\frac{g_2(\theta)}{g_2(x_1^*)}\right)\frac{1}{a_1(\theta)}d\theta + \int_{x_2^*}^{x_2} \left(1-\frac{g_1(\theta)}{g_1(x_2^*)}\right)\frac{1}{a_2(\theta)}d\theta,\\
V_3(x_1,x_2) &= \int_{x_1^*}^{x_1} \left(1-\frac{g_2(x_1^*)}{g_2(\theta)}\right)\frac{1}{f_1(\theta)}d\theta + \left[\int_{x_2^*}^{x_2} \left(1-\frac{g_1(x_2^*)}{g_1(\theta)}\right)\frac{1}{f_2(\theta)}d\theta\right]\frac{g_1(x_2^*)}{g_2(x_1^*)}.
\end{aligned} \tag{2.4}$$

However, a number of assumptions in [8], despite of having a general nature, are of a rather involved form, their applicability being subject of further investigation. To further establish the usefulness of the functionals V_1, V_2, V_3, Georgescu *et al.* have used them in [9] to prove the global stability of the positive equilibria for versions of (2.1) and (2.2) featuring a Richards growth term in place of the logistic one, in the form:

$$\begin{aligned}
\frac{dx_1}{dt} &= r_1x_1\left[A_1-\left(\frac{x_1}{K_1}\right)^p\right]+\frac{r_1b_{12}}{K_1}x_1x_2,\\
\frac{dx_2}{dt} &= r_2x_2\left[A_2-\left(\frac{x_2}{K_2}\right)^p\right]+\frac{r_2b_{21}}{K_2}x_1x_2,
\end{aligned} \tag{2.5}$$

and respectively:

$$\begin{aligned}
\frac{dx_1}{dt} &= r_1x_1A_1-\frac{r_1x_1^{p+1}}{K_1^p+b_{12}x_2},\\
\frac{dx_2}{dt} &= r_2x_2A_2-\frac{r_2x_2^{p+1}}{K_2^p+b_{21}x_1}.
\end{aligned} \tag{2.6}$$

In the above models, $A_1 = 1-\frac{e_1}{r_1}$, $A_2 = 1-\frac{e_2}{r_2}$ and $p \geq 1$, being assumed that $0 \leq e_1 < r_1$, $0 \leq e_2 < r_2$ and that $b_{12}, b_{21} > 0$, $K_1, K_2 > 0$ and being also observed that for $p = 1$ the models (2.5) and (2.6) reduce to (2.1) and (2.2), respectively. The global stability of the positive equilibrium of the following mutualistic model with restricted growth rates:

$$\begin{aligned}
\frac{dx_1}{dt} &= r_1x_1\left(1-\frac{x_1}{K_1}\right)+c_1x_1(1-e^{-\alpha_2x_2}),\\
\frac{dx_2}{dt} &= r_2x_2\left(1-\frac{x_2}{K_2}\right)+c_2x_2(1-e^{-\alpha_1x_1}),
\end{aligned} \tag{2.7}$$

proposed by Graves *et al.* in [10] has also been established in [9] by using Lyapunov's second method and the functional V_3.

One would think that the stability of the coexisting equilibria for two-species models of commensalism would follow immediately from the corresponding results for models of mutualism, when these results are available. After all, commensalism can be thought as mutualism in which one of the two interspecies interaction terms is zero, so at a glance everything should be simpler.

However, this is not actually the case. Even a cursory look at the specific forms of the functionals V_1, V_2, V_3 given in (2.4) (or of the functionals in [24], which are particular cases) shows that they cannot deal directly with the situation in which one or more of the functions f_1, f_2, g_1, g_2 are null, as either a denominator or one of the integrals is null. By replacing the problematic integral (null or with null denominator) with a logarithmic term, Vargas-De-León and Gómez-Alcaraz [25] have obtained global stability results for the positive equilibria of the models:

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right), \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \frac{r_2 b_{21}}{K_2} x_1 x_2, \end{aligned} \tag{2.8}$$

and:

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right), \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{K_2 + b_{21} x_1}\right), \end{aligned} \tag{2.9}$$

which are the direct commensalistic counterparts of (2.1) and (2.2). Although the use of logarithmic functionals to establish the stability of two-species models has a tradition which goes back to [26], one would, of course, think of a motivation of their use and what to use in place of a logarithm for different-looking two-species models. The Lyapunov functional V_1 has been introduced (up to a sign change) by Harrison in [13] to discuss the stability of a predator–prey interaction. Related functionals have been systematically employed by Korobeinikov [16, 17] to establish the stability of equilibria for general disease propagation models with abstract nonlinear incidence. See also [7], where the global dynamics of a SEIV model with nonlinear incidence of infection and removal has been studied using the same approach, employing a functional which is formally related to V_1 and [19], who discussed the stability of a SEIR model with varying infectivity and infinite delay. For related numerical aspects, see [5, 6, 18].

On the same line of thought, we continue here the investigation started in [9] and obtain the global stability of the positive equilibria for the models:

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left[1 - \left(\frac{x_1}{K_1}\right)^p\right], \\ \frac{dx_2}{dt} &= r_2 x_2 \left[1 - \left(\frac{x_2}{K_2}\right)^p\right] + \frac{r_2 b_{21}}{K_2} x_1 x_2, \end{aligned} \tag{2.10}$$

and respectively:

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left[1 - \left(\frac{x_1}{K_1}\right)^p\right], \\ \frac{dx_2}{dt} &= r_2 x_2 - \frac{r_2 x_2^{p+1}}{K_2^p + b_{21} x_1}, \end{aligned} \tag{2.11}$$

that is, for the commensalistic counterparts of (2.5) and (2.6), respectively, without harvesting (so that $e_1 = e_2 = 0$ and consequently $A_1 = A_2 = 1$), assuming that $p \geq 1$. We also establish the global stability of the positive equilibrium of the following commensalistic model with restricted growth rate:

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right), \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + c_2 x_2 (1 - e^{-\alpha_1 x_1}), \end{aligned} \tag{2.12}$$

that is, the commensalistic correspondent of (2.7).

Another motivation for studying commensalistic models separately is related to their criticism mentioned earlier. Even if commensalism is in reality a special form of strictly positive (but asymmetric) two-way interaction between species, a mathematical continuity argument can still use the commensalism stability results we derive in this paper as a good approximation. In other words, one can reasonably expect that a result for a commensalism model of type (2.3) with $g_1(x_2) = 0$ is a good approximation for a mutualistic model with $g_1(x_2)$ close to zero in a biologically suitable interval for x_2.

At the same time, it may not be possible to simply use pre-existing theorems proved for mutualistic models by simply adjusting the parameters to force one of these functions to be close to zero. This may be due to specific biological assumptions in situations where one of the species has a negligible effect on the other. Some arguments that criticize commensalism models mention the fact that at higher densities the apparently neutral species may have a nonzero effect on the other. For example, *epiphytes*, which are non-parasitic plants that grow attached to trees, may impede the photosynthesis of the host plant at very high densities (negative effect) or they may protect the bark of the host (positive effect) [1].

Therefore, it may not be possible to adjust, for example, a mutualistic model already studied to simulate a "near commensalism" situation. For example, in the mutualistic model with restricted growth rate (2.7), if the neutral species is given by x_2 then one cannot simply consider $g_1(x_2) = c_1(1 - e^{-\alpha_2 x_2})$ by using a c_1 close to zero to simulate a commensalism interaction since g_1 is a concave downward function which indicates that the impact rate of x_2 actually decreases with higher values of x_2 which is the opposite of what may happen in reality. Same remark can be made in the case of (2.5) and (2.6). In the first, g_1 would be a linear function which suggests that the impact rate of neutral species grows at a constant rate irrespective of its density; in the latter, g_1 is actually a decreasing function in x_2, again contrary to what may happen in a nearly-commensalistic interaction.

3. Algebraic Tools

We now introduce several inequalities which will be useful when evaluating the derivatives of Lyapunov functionals involved in the proofs of the stability results for the coexisting equilibria of (2.10)–(2.12). Their asymmetric nature is due to the asymmetric nature of the commensalistic models to which they are to be applied.

Lemma 3.1. *The following inequalities hold*:

(1) *If* $u > 0$ *and* $p \geq 0$, *then*

$$\left(1 - \frac{1}{u}\right)(1 - u^p) \leq 0, \tag{3.1}$$

with equality if $p = 0$ *and all* $u > 0$ *or if* $p > 1$ *and* $u = 1$.

(2) *If* $u, v > 0$ *and* $p \geq 1$, *then*

$$\left(1 - \frac{1}{u}\right)(1 - u^p) + \left(1 - \frac{1}{v}\right)(u - v^p) \leq 0, \tag{3.2}$$

with equality if and only if $u = v = 1$.

(3) *If* $u, v > 0$ *and* $p \geq 1$, *then*

$$\frac{1}{u^{p-1}}\left(1 - \frac{1}{u}\right)(1 - u^p) + \frac{1}{v^{p-1}}\left(1 - \frac{1}{v}\right)(u - v^p) \leq 0, \tag{3.3}$$

with equality if and only if $u = v = 1$.

(4) *If* $u, v > 0$ *and* $p \geq 1$, *then*

$$(u - 1)(1 - u^p) + (v - 1)(u - v^p) \leq 0, \tag{3.4}$$

with equality if and only if $u = v = 1$.

Proof. The first inequality is obvious, and so is its equality case. For the second one, let us denote

$$E_1 = \left(1 - \frac{1}{u}\right)(1 - u^p) + \left(1 - \frac{1}{v}\right)(u - v^p)$$

and observe that

$$\begin{aligned} E_1 &= \left(1 - \frac{1}{u}\right)(u - u^p) + \left(1 - \frac{1}{u}\right)(1 - u) + \left(1 - \frac{1}{v}\right)(v - v^p) + \left(1 - \frac{1}{v}\right)(u - v) \\ &= u\left(1 - \frac{1}{u}\right)(1 - u^{p-1}) + v\left(1 - \frac{1}{v}\right)(1 - v^{p-1}) + 3 - \frac{1}{u} - v - \frac{u}{v} \\ &= E_{11} + E_{12} + E_{13}. \end{aligned}$$

While $E_{11} \leq 0$ and $E_{12} \leq 0$ by (3.1), it is also seen that $E_{13} \leq 0$ by $AM - GM$ inequality (i.e. the inequality between the arithmetic mean and the geometric mean for two positive numbers). Since $E_{13} = 0$ if and only if $u = v = 1$, case which leads also to $E_{11} = E_{12} = 0$, it is seen that the equality case for (3.2) is $u = v = 1$. To prove (3.3), let us denote

$$E_2 = \frac{1}{u^{p-1}}\left(1 - \frac{1}{u}\right)(1 - u^p) + \frac{1}{v^{p-1}}\left(1 - \frac{1}{v}\right)(u - v^p)$$

and observe that

$$\begin{aligned} E_2 &= \frac{1}{u^{p-1}}\left(1 - \frac{1}{u}\right)(1 - u^{p-1}) + \frac{1}{u^{p-1}}\left(1 - \frac{1}{u}\right)(u^{p-1} - u^p) \\ &\quad + \frac{1}{v^{p-1}}\left(1 - \frac{1}{v}\right)(u - uv^{p-1}) + \frac{1}{v^{p-1}}\left(1 - \frac{1}{v}\right)(uv^{p-1} - v^p) \\ &= \frac{1}{u^{p-1}}\left(1 - \frac{1}{u}\right)(1 - u^{p-1}) + \left(1 - \frac{1}{u}\right)(1 - u) \\ &\quad + \frac{u}{v^{p-1}}\left(1 - \frac{1}{v}\right)(1 - v^{p-1}) + \left(1 - \frac{1}{v}\right)(u - v) \\ &= E_{21} + E_{22} + E_{23} + E_{24}. \end{aligned}$$

By (3.1), it is seen that $E_{21} \leq 0$ and $E_{23} \leq 0$. Also,

$$E_{22} + E_{24} = 3 - \frac{1}{u} - v - \frac{u}{v} \leq 0,$$

as seen above, by $AM - GM$ inequality, from which we also obtain that the equality case for (3.3) is $u = v = 1$. To deduce (3.4), let us denote

$$E_3 = (u - 1)(1 - u^p) + (v - 1)(u - v^p)$$

and observe that

$$\begin{aligned} E_3 &= (u - 1)(1 - u) + (u - 1)(u - u^p) + (v - 1)(u - v) + (v - 1)(v - v^p) \\ &= (-u^2 - v^2 + u + v - 1 + uv) + u^2\left(1 - \frac{1}{u}\right)(1 - u^{p-1}) \\ &\quad + v^2\left(1 - \frac{1}{v}\right)(1 - v^{p-1}) \\ &= -\frac{1}{2}[(u - 1)^2 + (v - 1)^2 + (u - v)^2] + u^2\left(1 - \frac{1}{u}\right)(1 - u^{p-1}) \\ &\quad + v^2\left(1 - \frac{1}{v}\right)(1 - v^{p-1}) \\ &= E_{31} + E_{32} + E_{33}. \end{aligned}$$

It is obvious that $E_{31} \leq 0$, while $E_{32} \leq 0$ and $E_{33} \leq 0$ by (3.1). Noting that $E_{31} = 0$ if and only if $u = v = 1$, the equality case for (3.4) is immediate. □

4. Commensalistic Models with Richards Growth

We start with an analysis of the models (2.10) and (2.11). It is easily seen that $(0,\infty)\times(0,\infty)$ is an invariant region for both of them. Also, the models (2.10) and (2.11) admit the coexisting equilibria $\mathbf{E_1^*}$ and $\mathbf{E_2^*}$, respectively, with:

$$\mathbf{E_1^*} = \left(K_1, \left(K_2^p + b_{21}K_1K_2^{p-1}\right)^{\frac{1}{p}}\right), \quad \mathbf{E_2^*} = \left(K_1, \left(K_2^p + b_{21}K_1\right)^{\frac{1}{p}}\right). \tag{4.1}$$

We shall now proceed with a stability analysis of the coexisting equilibria $\mathbf{E_1^*}$ and $\mathbf{E_2^*}$. Let us start with $\mathbf{E_1^*}$ and denote $\mathbf{E_1^*} = (x_1^*, x_2^*)$. It is seen that the components x_1^* and x_2^*, given in (4.1) also satisfy the following equilibrium relation

$$1 + \frac{b_{21}}{K_2}x_1^* = \left(\frac{x_2^*}{K_2}\right)^p. \tag{4.2}$$

For the proof of our stability results, we shall employ Lyapunov's second method. We now give a motivation regarding the specific form of the functional we are going to employ. It has been observed in [9] that the following particular form of V_3:

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

can be used to prove the global stability of the positive equilibrium of (2.5), that is, of a mutualistic version of (2.10) with harvesting, for the following choice of f_1, f_2, f_3 and f_4 in the abstract framework (2.3):

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

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

To construct our Lyapunov functional using V_3 as a template, we note that, for our model (2.10), $b_{12} = 0$ and g_1 is null. Although the abstract form of V_3 given in (2.4) involves the fraction $\frac{g_1(x_2^*)}{g_1(\theta)}$ in the second integral (which is the troublesome one), the integrand can be left unchanged in the concrete form of V_3 given above if one thinks that the simplification of b_{12} (which is now 0) occurs beforehand. The coefficient of the second integral is also 0, but there is no possibility of having a Lyapunov functional consisting of the first integral alone, so we may need a positive constant defined *ad hoc* in place of b_{12}. This heuristic argument leads us to using the Lyapunov functional

$$U_3(x_1,x_2) = \int_{x_1^*}^{x_1}\left(1 - \frac{x_1^*}{\theta}\right)\frac{1}{\theta}d\theta + \frac{r_1\alpha K_2x_2^*}{r_2b_{21}K_1x_1^*}\left[\int_{x_2^*}^{x_2}\left(1 - \frac{x_2^*}{\theta}\right)\frac{1}{\theta}d\theta\right]$$

(we have chosen the subscript to stress the originating template functional, although there are no U_1 and U_2 defined as of yet), where $\alpha > 0$ will be determined later on by matching coefficients. It is of no surprise to remark that the coexisting equilibrium $\mathbf{E_1^*}$ preserves the global asymptotic stability property which has been proved in [9] for the mutualistic counterpart of (2.10).

Theorem 4.1. *The coexisting equilibrium* $\mathbf{E}_1^*$ *is globally asymptotically stable in* $(0,\infty)\times(0,\infty)$.

Proof. First, it is seen that U_3 increases whenever any of $|x_1 - x_1^*|$ and $|x_2 - x_2^*|$ increases and that $U_3(x_1,x_2)\geq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. Also, the level sets of U_3 do not have limit points on the boundary of $(0,\infty)\times(0,\infty)$, since $U_3(x_1,x_2)$ tends to ∞ if either x_1 or x_2 tends to 0 or to ∞.

We now evaluate the derivative of U_3 along the solutions of (2.10). One sees that

$$\begin{aligned}\dot{U}_3 &= \left(1-\frac{x_1^*}{x_1}\right)\frac{1}{x_1}\frac{dx_1}{dt} + \frac{r_1\alpha K_2 x_2^*}{r_2 b_{21}K_1 x_1^*}\left(1-\frac{x_2^*}{x_2}\right)\frac{1}{x_2}\frac{dx_2}{dt}\\ &= r_1\left(1-\frac{x_1^*}{x_1}\right)\left[1-\left(\frac{x_1}{K_1}\right)^p\right]\\ &\quad + \frac{r_1\alpha K_2 x_2^*}{b_{21}K_1 x_1^*}\left(1-\frac{x_2^*}{x_2}\right)\left[1-\left(\frac{x_2}{K_2}\right)^p + \frac{b_{21}x_1}{K_2}\right]. \end{aligned} \tag{4.3}$$

By the equilibrium condition (4.2), one sees that

$$\left(1+\frac{b_{21}}{K_2}x_1^*\right)\left(\frac{K_2}{x_2^*}\right)^p = 1$$

and consequently, by substituting this relation into the right-hand side of (4.3) and recalling from (4.1) that $x_1^* = K_1$, we obtain

$$\begin{aligned}\dot{U}_3 &= r_1\left(1-\frac{x_1^*}{x_1}\right)\left[1-\left(\frac{x_1}{x_1^*}\right)^p\right]\\ &\quad + \frac{r_1\alpha K_2 x_2^*}{b_{21}(x_1^*)^2}\left(1-\frac{x_2^*}{x_2}\right)\left[1-\left(\frac{x_2}{x_2^*}\right)^p\left(1+\frac{b_{21}}{K_2}x_1^*\right)+\frac{b_{21}x_1}{K_2}\right]\\ &= r_1\left(1-\frac{x_1^*}{x_1}\right)\left[1-\left(\frac{x_1}{x_1^*}\right)^p\right] + \frac{r_1\alpha K_2 x_2^*}{b_{21}(x_1^*)^2}\left(1-\frac{x_2^*}{x_2}\right)\left[1-\left(\frac{x_2}{x_2^*}\right)^p\right]\\ &\quad + \left(1-\frac{x_2^*}{x_2}\right)\frac{r_1\alpha x_2^*}{x_1^*}\left[\frac{x_1}{x_1^*}-\left(\frac{x_2}{x_2^*}\right)^p\right]\\ &= T_1 + T_2 + T_3. \end{aligned} \tag{4.4}$$

By inequality (3.1) of Lemma 3.1, we observe that $T_2 \leq 0$. Let us now choose $\alpha = \frac{x_1^*}{x_2^*}$, so that $\frac{\alpha x_2^*}{x_1^*} = 1$. Then, by inequality (3.2) of Lemma 3.1 with $u = \frac{x_1}{x_1^*}$ and $v = \frac{x_2}{x_2^*}$, we obtain that $T_1 + T_3 \leq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. The use of LaSalle's invariance theorem completes the proof of Theorem 4.1. □

We now turn our attention to the stability of $\mathbf{E}_2^*$. Let us denote again $\mathbf{E}_2^* = (x_1^*, x_2^*)$, for an easier construction of the functional through similarity with the templates given in (2.4), since there is no danger of confusion with the coordinates of $\mathbf{E_1^*}$. It is seen that x_1^* and x_2^* satisfy the following equilibrium relation

$$\frac{K_2^p + b_{21}x_1^*}{(x_2^*)^p} = 1. \tag{4.5}$$

It has been observed in [9] that the following particular form of V_1:

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

can be used to prove the global stability of the positive equilibrium of (2.6), that is, of the mutualistic version of (2.11). Since one could consider again that $b_{12} = 0$, by a heuristic argument similar to the one displayed above and noting that now $A_1 = A_2 = 1$, one could use the functional

$$U_1(x_1,x_2) = \frac{b_{21}}{(x_2^*)^p r_1}\int_{x_1^*}^{x_1} \frac{\theta - x_1^*}{\big(K_2^p + b_{21}\theta\big)\theta^{p+1}}d\theta + \frac{\alpha}{(x_1^*)^p r_2}\int_{x_2^*}^{x_2} \frac{\theta - x_2^*}{K_1^p\theta^{p+1}}d\theta,$$

where $\alpha > 0$ shall be determined later on by matching coefficients.

Theorem 4.2. *The coexisting equilibrium* $\mathbf{E_2^*}$ *is globally asymptotically stable in* $(0,\infty)\times(0,\infty)$.

Proof. First, it is seen that U_1 increases whenever any of $|x_1 - x_1^*|$ and $|x_2 - x_2^*|$ increases and that $U_1(x_1,x_2) \geq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. Also, the level sets of U_1 do not have limit points on the boundary of $(0,\infty)\times(0,\infty)$ since $U_1(x_1,x_2)$ tends to ∞ if either x_1 or x_2 tends to 0 or to ∞.

We now evaluate the derivative of U_1 along the solutions of (2.10). One sees that

$$\begin{aligned}\dot{U}_1 &= \frac{b_{21}}{(x_2^*)^p r_1}\frac{x_1 - x_1^*}{\big(K_2^p + b_{21}x_1\big)x_1^{p+1}}\frac{dx_1}{dt} + \frac{\alpha}{(x_1^*)^p r_2}\frac{x_2 - x_2^*}{K_1^p x_2^{p+1}}\frac{dx_2}{dt}\\ &= \frac{b_{21}}{(x_2^*)^p}\frac{x_1 - x_1^*}{\big(K_2^p + b_{21}x_1\big)x_1^p}\left[1 - \left(\frac{x_1}{x_1^*}\right)^p\right]\\ &\quad + \frac{\alpha}{K_1^p(x_1^*)^p}\frac{x_2 - x_2^*}{\big(K_2^p + b_{21}x_1\big)x_2^p}\big(K_2^p + b_{21}x_1 - x_2^p\big).\end{aligned} \tag{4.6}$$

By substituting (4.5) into the right-hand side of (4.6), it is then seen that

$$\begin{aligned}\dot{U}_1 &= \frac{b_{21}}{(x_2^*)^p}\frac{x_1 - x_1^*}{\big(K_2^p + b_{21}x_1\big)x_1^p}\left[1 - \left(\frac{x_1}{x_1^*}\right)^p\right]\\ &\quad + \frac{\alpha}{K_1^p(x_1^*)^p}\frac{x_2 - x_2^*}{\big(K_2^p + b_{21}x_1\big)x_2^p}\left(K_2^p + b_{21}x_1 - \frac{K_2^p + b_{21}x_1^*}{(x_2^*)^p}x_2^p\right)\\ &= \frac{b_{21}}{(x_2^*)^p}\frac{x_1 - x_1^*}{\big(K_2^p + b_{21}x_1\big)x_1^p}\left[1 - \left(\frac{x_1}{x_1^*}\right)^p\right]\end{aligned}$$

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

We now evaluate the signs of T_2 and of T_1+T_3 with the help of Lemma 3.1, choosing in the process the right value for α. We observe that

$$
T_2=\frac{\alpha}{K_1^p (x_1^*)^p}\frac{K_2^p}{\left(K_2^p+b_{21}x_1\right)x_2^{p-1}}\left(1-\frac{x_2^*}{x_2}\right)\left[1-\left(\frac{x_2}{x_2^*}\right)^p\right]\le 0,
$$

by inequality (3.1) of Lemma 3.1. Also,

$$
\begin{aligned}
T_1+T_3={}&\frac{b_{21}}{\left(K_2^p+b_{21}x_1\right)(x_2^*)^p(x_1^*)^{p-1}}\left\{\left(\frac{x_1^*}{x_1}\right)^{p-1}\left(1-\frac{x_1^*}{x_1}\right)\left[1-\left(\frac{x_1}{x_1^*}\right)^p\right]\right.\\
&\left.+\frac{\alpha x_2^*}{(x_1^*)^p}\left(1-\frac{x_2^*}{x_2}\right)\left(\frac{x_2^*}{x_2}\right)^{p-1}\left[\frac{x_1}{x_1^*}-\left(\frac{x_2}{x_2^*}\right)^p\right]\right\}.
\end{aligned}
$$

Let us now choose $\alpha=\frac{(x_1^*)^p}{x_2^*}$, so that $\frac{\alpha x_2^*}{(x_1^*)^p}=1$. Then

$$
\begin{aligned}
T_1+T_3={}&\frac{b_{21}}{\left(K_2^p+b_{21}x_1\right)(x_2^*)^p(x_1^*)^{p-1}}\left\{\left(\frac{x_1^*}{x_1}\right)^{p-1}\left(1-\frac{x_1^*}{x_1}\right)\left[1-\left(\frac{x_1}{x_1^*}\right)^p\right]\right.\\
&\left.+\left(\frac{x_2^*}{x_2}\right)^{p-1}\left(1-\frac{x_2^*}{x_2}\right)\left[\frac{x_1}{x_1^*}-\left(\frac{x_2}{x_2^*}\right)^p\right]\right\}\\
\le{}&0,
\end{aligned}
$$

by inequality (3.3) of Lemma 3.1 with $u=\frac{x_1}{x_1^*}$ and $v=\frac{x_2}{x_2^*}$. It is also to be noted that $T_1+T_3=0$ if and only if $x_1=x_1^*$ and $x_2=x_2^*$. The use of LaSalle's invariance theorem completes the proof. □

Let us now provide an alternate proof of Theorem 4.2, this time using as a template the remaining mutualistic Lyapunov functional, V_2. It has been observed in [9] that the following particular form of V_2:

$$
V_2(x_1,x_2)=\frac{b_{21}}{r_1A_1}\int_{x_1^*}^{x_1}\frac{\theta-x_1^*}{\left(K_2^p+b_{21}\theta\right)\theta}d\theta+\frac{b_{12}}{r_2A_2}\int_{x_2^*}^{x_2}\frac{\theta-x_2^*}{\left(K_1^p+b_{12}\theta\right)\theta}d\theta
$$

is of use to prove the global stability of the positive equilibrium of (2.6), that is, of the mutualistic version of (2.11). Motivated by this specific form of V_2 and keeping in mind that now $A_1 = A_2 = 1$, we shall attempt to use the following Lyapunov functional

$$U_2(x_1, x_2) = \frac{b_{21}}{r_1}\int_{x_1^*}^{x_1} \frac{\theta - x_1^*}{(K_2^p + b_{21}\theta)\theta} d\theta + \frac{\alpha}{r_2}\int_{x_2^*}^{x_2} \frac{\theta - x_2^*}{K_1^p \theta} d\theta,$$

where $\alpha > 0$ will be determined, as usual, by coefficient matching. We now evaluate the derivative of U_2 along the solutions of (2.11). It is seen that

$$\begin{aligned} \dot{U}_2 &= \frac{b_{21}}{r_1}\frac{x_1 - x_1^*}{\big(K_2^p + b_{21}x_1\big)x_1}\frac{dx_1}{dt} + \frac{\alpha}{r_2}\frac{x_2 - x_2^*}{K_1^p x_2}\frac{dx_2}{dt} \\ &= \frac{b_{21}}{K_2^p + b_{21}x_1}\big(x_1 - x_1^*\big)\left[1 - \left(\frac{x_1}{x_1^*}\right)\right]^p \\ &\quad + \frac{\alpha}{K_1^p}\big(x_2 - x_2^*\big)\frac{1}{K_2^p + b_{21}x_1}\big(K_2^p + b_{21}x_1 - x_2^p\big). \end{aligned}$$

Using again the equilibrium relation (4.5), we observe that

$$\begin{aligned} \dot{U}_2 &= \frac{b_{21}}{K_2^p + b_{21}x_1}\big(x_1 - x_1^*\big)\left[1 - \left(\frac{x_1}{x_1^*}\right)^p\right] + \frac{\alpha}{K_1^p}\frac{x_2 - x_2^*}{K_2^p + b_{21}x_1}K_2^p\left[1 - \left(\frac{x_2}{x_2^*}\right)^p\right] \\ &\quad + \frac{\alpha}{K_1^p}\frac{x_2 - x_2^*}{K_2^p + b_{21}x_1}b_{21}x_1^*\left[\frac{x_1}{x_1^*} - \left(\frac{x_2}{x_2^*}\right)^p\right] \\ &= T_1 + T_2 + T_3. \end{aligned}$$

We observe that

$$T_2 = \frac{\alpha}{K_1^p x_2}\frac{K_2^p}{K_2^p + b_{21}x_1}\left(1 - \frac{x_2^*}{x_2}\right)\left[1 - \left(\frac{x_2}{x_2^*}\right)^p\right] \leq 0,$$

by inequality (3.1) of Lemma 3.1. Also,

$$T_1 + T_3 = \frac{b_{21}x_1^*}{K_2^p + b_{21}x_1}\left\{\left(\frac{x_1}{x_1^*} - 1\right)\left[1 - \left(\frac{x_1}{x_1^*}\right)^p\right] + \frac{\alpha x_2^*}{K_1^p}\left(\frac{x_2}{x_2^*} - 1\right)\left[\frac{x_1}{x_1^*} - \left(\frac{x_2}{x_2^*}\right)^p\right]\right\}.$$

Choosing now $\alpha = \frac{K_1^p}{x_2^*}$, so that $\frac{\alpha x_2^*}{K_1^p} = 1$, it follows by inequality (3.4) of Lemma 3.1 that $T_1 + T_3 \leq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. The use of LaSalle's invariance principle finishes this alternate proof.

5. A Commensalistic Model with Restricted Growth Rates

We now discuss the stability properties of the model (2.12). Again, it is easily seen that $(0, \infty) \times (0, \infty)$ is an invariant region for (2.12). Also, (2.12) admits the positive equilibrium $\mathbf{E_3^*} = \big(x_1^*, x_2^*\big)$, given by

$$\mathbf{E_3^*} = \left(K_1, K_2\left(1 + \frac{c_2}{r_2}\Big(1 - e^{-\alpha_1 K_1}\Big)\right)\right). \tag{5.1}$$

Note that x_1^* and x_2^* also satisfy the following equilibrium relation

$$1 = \frac{x_2^*}{K_2} - \frac{c_2}{r_2}(1 - e^{-\alpha_1 x_1^*}). \tag{5.2}$$

It has been observed in [9] that the following particular form of V_3:

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

is of use to prove the global stability of the positive equilibrium of (2.7), that is, of the mutualistic version of (2.12).

To define the suitable Lyapunov functional for our model of commensalism, the problem is twofold, since now two coefficients, c_1 and α_2, are null. Among these, c_1 is not paired (i.e. it does not appear both at the denominator and the numerator of a fraction). Noting that a Lyapunov functional remains a Lyapunov functional after multiplication with a nonzero constant and taking a few formal limits for $\alpha_2 \to 0$ inside the second integral (again, the problematic one), we arrive at the following tentative Lyapunov functional

$$\widetilde{U_3}(x_1, x_2) = c_1 \int_{x_1^*}^{x_1} \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 \theta}}{1 - e^{-\alpha_1 \theta}} \frac{1}{\theta} d\theta + \left(\int_{x_2^*}^{x_2} \left(1 - \frac{x_2^*}{\theta}\right) \frac{1}{\theta} d\theta \right) \frac{\alpha}{1 - e^{-\alpha_1 x_1^*}},$$

where $\alpha > 0$ will be determined later on by the usual procedure.

Theorem 5.1. *The coexisting equilibrium* $\mathbf{E_3^*}$ *is globally asymptotically stable in* $(0, \infty) \times (0, \infty)$.

Proof. First, it is seen that $\widetilde{U_3}$ increases whenever any of $|x_1 - x_1^*|$ and $|x_2 - x_2^*|$ increases and that $\widetilde{U_3}(x_1, x_2) \geq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. Also, the level sets of $\widetilde{U_3}$ do not have limit points on the boundary of $(0, \infty) \times (0, \infty)$ since $\widetilde{U_3}(x_1, x_2)$ tends to ∞ if either x_1 or x_2 tends to 0 or to ∞.

We now evaluate the derivative of $\widetilde{U_3}$ along the solutions of (2.12). It is seen that

$$\begin{aligned} \dot{\widetilde{U_3}} &= c_2 \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} \frac{1}{x_1} \frac{dx_1}{dt} + \left(1 - \frac{x_2^*}{x_2}\right) \frac{1}{x_2} \frac{\alpha}{1 - e^{-\alpha_1 x_1^*}} \frac{dx_2}{dt} \\ &= c_2 \frac{e^{-\alpha_1 x_1^*} - e^{-\alpha_1 x_1}}{1 - e^{-\alpha_1 x_1}} r_1 \left(1 - \frac{x_1}{K_1}\right) \\ &\quad + \left(1 - \frac{x_2^*}{x_2}\right) \frac{\alpha}{1 - e^{-\alpha_1 x_1^*}} r_2 \left[1 - \frac{x_2}{K_2} + \frac{c_2}{r_2}(1 - e^{-\alpha_1 x_1})\right] \\ &= T_1 + T_2. \end{aligned}$$

Evaluating the second term T_2, we observe that

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

It is seen that $T_{21}\le 0$, with equality if and only if $x_2 = x_2^*$, by inequality (3.1) of Lemma 3.1 or by $AM - GM$ inequality. Also,

$$\begin{aligned}
T_{22} &= \left(1-\frac{x_2^*}{x_2}\right)\frac{\alpha c_2}{1-e^{-\alpha_1 x_1^*}}\left[\frac{r_2}{c_2}\left(\frac{x_2}{x_2^*}-\frac{x_2}{K_2}\right)+(1-e^{-\alpha_1 x_1})\right]\\
&= \left(1-\frac{x_2^*}{x_2}\right)\frac{\alpha c_2}{1-e^{-\alpha_1 x_1^*}}\left[\frac{r_2}{c_2}\frac{x_2}{x_2^*}\left(1-\frac{x_2^*}{K_2}\right)+(1-e^{-\alpha_1 x_1})\right]. \qquad (5.3)
\end{aligned}$$

By the equilibrium relations (5.2) and (5.3), it is seen that

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

Let us now define:

$$\Phi : (0,\infty)\to(0,\infty), \quad \Phi(x) = \frac{1-e^{-\alpha_1 x}}{x}.$$

Noting that

$$\Phi'(x) = -\frac{e^{-\alpha_1 x}}{x^2}\big(e^{\alpha_1 x}-(1+\alpha_1 x)\big) < 0,$$

it follows that Φ is strictly decreasing on $(0,\infty)$. With this notation,

$$T_{22} = \left(1-\frac{x_2^*}{x_2}\right)\alpha c_2\left(-\frac{x_2}{x_2^*}+\frac{\Phi(x_1)x_1}{\Phi(x_1^*)x_1^*}\right).$$

Recalling that, by (5.1), $x_1^* = K_1$, we obtain

$$T_1 = c_2\left(1-\frac{1-e^{-\alpha_1 x_1^*}}{1-e^{-\alpha_1 x_1}}\right)r_1\left(1-\frac{x_1}{K_1}\right) = c_2\left(1-\frac{\Phi(x_1^*)x_1^*}{\Phi(x_1)x_1}\right)r_1\left(1-\frac{x_1}{x_1^*}\right).$$

This leads to

$$\begin{aligned}
T_1 + T_{22} &= c_2 \left(1 - \frac{\Phi(x_1^*)x_1^*}{\Phi(x_1)x_1}\right) r_1 \left(1 - \frac{x_1}{x_1^*}\right) \\
&\quad + \left(1 - \frac{x_2^*}{x_2}\right) \alpha c_2 \left(-\frac{x_2}{x_2^*} + \frac{\Phi(x_1)x_1}{\Phi(x_1^*)x_1^*}\right) \\
&= c_2 r_1 \left(1 - \frac{x_1}{x_1^*} - \frac{\Phi(x_1^*)x_1^*}{\Phi(x_1)x_1} + \frac{\Phi(x_1^*)}{\Phi(x_1)}\right) \\
&\quad + \alpha c_2 \left(-\frac{x_2}{x_2^*} + \frac{\Phi(x_1)x_1}{\Phi(x_1^*)x_1^*} + 1 - \frac{x_2^*}{x_2}\frac{\Phi(x_1)x_1}{\Phi(x_1^*)x_1^*}\right) \\
&= c_2 r_1 \left(1 - \frac{x_1}{x_1^*} - \frac{\Phi(x_1^*)x_1^*}{\Phi(x_1)x_1} + \frac{\Phi(x_1^*)}{\Phi(x_1)}\right) \\
&\quad + \alpha c_2 \left(3 - \frac{x_2}{x_2^*} - \frac{x_2^*}{x_2}\frac{\Phi(x_1)x_1}{\Phi(x_1^*)x_1^*} - \frac{\Phi(x_1^*)x_1^*}{\Phi(x_1)x_1}\right) \\
&\quad + \alpha c_2 \left(\frac{\Phi(x_1^*)x_1^*}{\Phi(x_1)x_1} + \frac{\Phi(x_1)x_1}{\Phi(x_1^*)x_1^*} - 2\right) \\
&= S_1 + S_2 + S_3.
\end{aligned}$$

Note that $S_2 \leq 0$, by $AM - GM$ inequality, and that $S_2 = 0$ if and only if $x_2 = x_2^*$ and $\Phi(x_1)x_1 = \Phi(x_1^*)x_1^*$, which leads to $x_1 = x_1^*$. Let us now choose $\alpha = r_1$, so that $c_2 r_1 = \alpha c_2$. Then

$$\begin{aligned}
S_1 + S_3 &= c_2 r_1 \left(-1 - \frac{x_1}{x_1^*} + \frac{\Phi(x_1^*)}{\Phi(x_1)} + \frac{\Phi(x_1)x_1}{\Phi(x_1^*)x_1^*}\right) \\
&= c_2 r_1 \left[\frac{x_1}{x_1^*}\left(\frac{\Phi(x_1)}{\Phi(x_1^*)} - 1\right) - \frac{\Phi(x_1^*)}{\Phi(x_1)}\left(\frac{\Phi(x_1)}{\Phi(x_1^*)} - 1\right)\right] \\
&= c_2 r_1 \frac{x_1}{x_1^*}\left(\frac{\Phi(x_1)}{\Phi(x_1^*)} - 1\right)\left(1 - \frac{\Phi(x_1^*)x_1^*}{\Phi(x_1)x_1}\right) \\
&\leq 0,
\end{aligned}$$

since Φ is decreasing, while $\Psi : (0, \infty) \to (0, \infty)$, $\Psi(x) = x\Phi(x) = 1 - e^{-\alpha_1 x}$ is increasing. By the previous analysis of the signs of S_2 and T_{21}, it follows that $\dot{U}_3 \leq 0$, with equality if and only if $x_1 = x_1^*$ and $x_2 = x_2^*$. The use of LaSalle's invariance principle finishes the proof of Theorem 5.1. $\square$

6. A Caveat

Having in view the particular forms of (2.8)–(2.11) and, in fact, the general structure of any model of commensalism, in which one equation is decoupled from the other, one may erroneously rest assured that as the solution of the "simple" equation converges to its steady state (monotonically, more so), the convergence of the solution of the other equation is quite an easy exercise, perhaps under suitable monotonicity assumptions. Why would then one need any other approach at all?

However, that is not always the case. Particularly, the convergence of the solution of the "simple" equation does not inherently mitigate unboundedness, which always lingers as a possible outcome in mutualistic and commensalistic systems. Below is an example of a planar system that is related to [22, Example 2.8], slightly modified to produce a model that can be interpreted as a commensalistic interaction between two species (to this purpose, note that the interaction term in the right-hand side of the second equation of (6.1) is always positive, being null if the size of the first species is equal to 0), but in which the limiting argument does not work as expected:

$$\begin{cases} x' = -x + 1, \\ y' = -y(y-1)(5-y) + yx(x-1)^2. \end{cases} \tag{6.1}$$

A biological interpretation is that species y, the one which benefits from the mutualistic interaction has a feasible domain $[0, 5]$. In other words, we do not allow an initial value for y greater than 5.

If one attempts to solve x first and then use its limit in the second equation, the "conclusion" would be that $(1, 1)$ is a globally stable equilibrium (i.e. global in the feasible domain $x > 0$ and $0 < y < 5$).

However this "conclusion" would not be true. The basin of attraction of $(1, 1)$ is not the same as far as y is concerned. In fact, this basin of attraction can be made arbitrarily small by letting the initial value x_0 be large enough. Furthermore, y may even become unbounded, as seen below.

Solving for x we obtain from the second equation that

$$x(t) = (x_0 - 1)e^{-t} + 1.$$

Thus, the first equation can be viewed as a non-autonomous single ODE, in the form

$$y' = \left\{-(y-1)(5-y) + \left[(x_0 - 1)e^{-t} + 1\right](x_0 - 1)^2 e^{-2t}\right\}y.$$

Looking at the expression in the square brackets, we see that $-(y-1)(5-y) < 0$ for $1 < y < 5$. However if x_0 is chosen large enough, then initially, while t is still close to zero, the negative component is canceled and y' remains positive until y increases past 5. Later on, as t increases, the effect of x_0 is no longer important, but since $y(t)$ increased past 5, then y' remains positive, and therefore $y(t) \to \infty$.

This calls for a higher degree of attention in the formalization of the limiting procedure, and we shall achieve that in the next section, in the context of asymptotically autonomous systems.

7. The Asymptotically Autonomous Systems Approach

Apart from using Lyapunov's second method, we may also use the theory of asymptotically autonomous systems to discuss the global stability of positive equilibria for models of mutualism. To establish the framework for our approach, let us consider the following differential systems:

$$x' = f(x, t) \tag{7.1}$$

and

$$x' = g(x), \tag{7.2}$$

with t being the independent variable, $t \in \mathbb{R}$, and $x \in \mathbb{R}^n$. We say that (7.1) is asymptotically autonomous with limiting system (7.2) if

$$f(x, t) \to g(x) \quad \text{as } t \to \infty, \text{ locally uniformly with respect to } x \in \mathbb{R}^n.$$

The idea behind the use of asymptotically autonomous systems is often not to remove the explicit dependence on t, since most models are already autonomous to begin with, but rather to reduce the initial problem to a lower-dimensional one which is significantly more tractable. However, extensive work done by Thieme and his coworkers (see, for instance, [2] and references therein) shows that the behavior of the limiting system may not always coincide with that of the original one and specific conditions need to be imposed for this purpose. In this regard, we provide below [2, Theorems 2.3 and 2.5], which characterize the connection between the original and the limiting system in terms of the asymptotic behavior of orbits.

Theorem 7.1. *Let e be a locally asymptotically stable equilibrium of* (7.2) *and W its basin of attraction. Then every pre-compact orbit of* (7.1) *whose ω-limit set intersects W converges to e.*

Theorem 7.2. *Let e_1 and e_2 be two equilibria of* (7.2). *Assume that the space of solutions* ($\mathbb{R}^n$) *is the disjoint union of a closed set X_1 and an open set X_2 both forward-invariant under the flow of* (7.1) *and* (7.2) *such that $e_1 \in X_1$ and $e_2 \in X_2$. Assume that e_2 is locally stable for* (7.2) *and e_1 is locally stable for the restriction of* (7.2) *to X_1. Assume also that e_1 is a weak repeller under the flow of* (7.1) (*i.e. no forward orbit of* (7.1) *starting in X_2 converges to e_1*). *Then every pre-compact orbit of* (7.1) *starting in X_i converges to e_i.*

The important difference between these results is that only the second one (which contains stronger assumptions) guarantees that the behavior of solutions of the limiting system matches that of the original. Note that the first theorem does not guarantee that the basins of attraction for e coincide between the two systems. Counterexamples to that effect are provided in [2].

For our purpose, we take advantage of the fact that, in a model of commensalism, the species that does not benefit from the other one can be analyzed separately and have its asymptotic behavior characterized. Consequently, the equation modeling the behavior of the second species can be considered as an asymptotically autonomous differential equation, eligible for a treatment via the results mentioned above.

7.1. *A particular case*

Let us consider the following two-dimensional models of commensalistic interactions

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \dfrac{x_1}{K_1}\right), \\ x_2' = r_2 x_2 \left(\dfrac{x_2}{A_2} - 1\right)\left(1 - \dfrac{x_2}{K_2}\right) + \dfrac{r_2 b_{21}}{K_2} x_1 x_2 \end{cases} \tag{7.3}$$

and

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \dfrac{x_1}{K_1}\right), \\ x_2' = r_2 x_2 \left(\dfrac{x_2}{A_2} - 1\right)\left(1 - \dfrac{x_2}{K_2}\right) + c_2(1 - e^{-\alpha_1 x_1}) x_2, \end{cases} \tag{7.4}$$

that is, versions of (2.8) and (2.12), respectively, with strong Allee effects.

In what follows, we shall analyze them together by using the slightly more general framework

$$\begin{cases} x' = ax\left(1 - \dfrac{x}{K}\right), \\ y' = by\left(\dfrac{y}{A} - 1\right)\left(1 - \dfrac{y}{T}\right) + f(x)y, \end{cases} \tag{7.5}$$

where $f(x)$ is a continuous and positive-valued function, $a > 0$, $b > 0$, $K > 0$ and $T > A > 0$.

Since $a > 0$, it follows that $x(t) \to K$ as $t \to \infty$ and the second equation becomes an asymptotically autonomous ODE:

$$y' = g(t, y) := by\left(\frac{y}{A} - 1\right)\left(1 - \frac{y}{T}\right) + f(x(t))y, \tag{7.6}$$

its limiting ODE being given by

$$y' = h(y) := by\left(\frac{y}{A} - 1\right)\left(1 - \frac{y}{T}\right) + f(K)y. \tag{7.7}$$

Since

$$|g(t, y) - h(y)| = |f(x(t)) - f(K)||y|,$$

it is seen that $g(t, y)$ converges locally uniformly to $h(y)$.

The equilibria of (7.7) are 0 and any possible real root of the quadratic equation is

$$-\frac{b}{AT}y^2 + \left(\frac{b}{A} + \frac{b}{T}\right)y + f(K) - b = 0. \tag{7.8}$$

Since the discriminant of (7.8) is

$$\Delta = \left(\frac{b}{A} - \frac{b}{T}\right)^2 + \frac{4b}{AT}f(K) > 0,$$

(7.8) has two real roots, which we may denote by y_1 and y_2, $y_1 < y_2$. We notice that $y_1 + y_2 > 0$, and hence at least one of the roots is >0.

Case 1. $f(K) > b$

In this case, $y_1 < 0$ and $y_2 > 0$. Furthermore, $h(y) > 0$ if $0 < y < y_2$ and $h(y) < 0$ if $y > y_2$, which implies that y_2 is a globally stable equilibrium for the limiting ODE (7.7).

We now prove that the solutions of (7.6) also converge to this equilibrium. First, notice that $[0, \infty)$, the space of solutions of (7.7), is the disjoint union of the closed set $X_1 = \{0\}$ and of the open set $X_2 = (0, \infty)$, each of them containing the two equilibria, $e_1 = 0$ and $e_2 = y_2$ respectively. It is also easy to see that these two sets are forward-invariant under the flow of both (7.7) and (7.6).

Furthermore, 0 is a weak repeller for the asymptotically autonomous semi-flow given by (7.6). This happens since if $y(t) \to 0$ with $y(0) > 0$, then

$$\frac{y'}{y} \to -b + f(K) > 0$$

and $y(t)$ goes away from 0. Consequently, all conditions of Theorem 7.2 are met, which means that all solutions of (7.6) converge to 0 or y_2 and each of these equilibria has the same basin of attraction as in (7.7). Since the basin of attraction of y_2 is the entire positive real line, it follows that y_2 is a globally stable equilibrium point for (7.6).

Remark 7.3. This case provides a threshold for the commensalism effect to overcome the Allee effect of the species that benefits from the presence of the other. Actually, when (x, y) approaches $(K, 0)$, $f(K)$ approximates the positive effects of the mutualistic interaction upon the per capita growth rate of the second species, while $-b$ approximates the (negative) per capita growth rate in the absence of mutualism. If $f(K) > b$, the positive effects dominate and the second species is able to escape extinction.

To the contrary, the second case analyzed below shows that, if this condition fails, the Allee effect is preserved, even though the basin of attraction for the extinction steady state is still affected by the presence of commensalism.

Case 2. $f(K) < b$

In this case, both y_1 and y_2 are positive. Furthermore, since $h(y) > 0$ for $y_1 < y < y_2$ and negative otherwise, it follows that for the limiting ODE (7.7) both 0 and y_2 are locally stable, while y_1 is unstable. In other words, if $0 < y < y_1$, then $y \to 0$ and if $y > y_1$, then $y \to y_2$. Hence the basin of attraction for 0 is $[0, y_1)$ and for y_2 is (y_1, ∞). Any solution of (7.6) starting at a point different than y_1 will necessarily intersect one of these two intervals. By Theorem 7.1, any solution of (7.7) starting at a point different than y_1 will then approach 0 or y_2.

However, the conditions of Theorem 7.2 are not met (in particular, (y_1, ∞) is not invariant under the flow of the asymptotically autonomous ODE).

7.2. *The general case*

We can further generalize the framework within (7.3) and (7.4) may be treated by employing a generic function for the per capita growth rate (i.e. without a separation for the birth and the death rate), in the following form

$$\begin{cases} x_1' = r_1 x_1 h_1(x_1), \\ x_2' = r_2 x_2 h_2(x_2, x_1). \end{cases} \tag{7.9}$$

Let us consider the following assumptions upon the continuous functions h_1 and h_2:

- (C1) $h_1(x_1) < 0$ for all $x_1 > K_1$.
- (C2) $h_2(0, 0) \geq 0$ and $h_2(x_2, 0) < 0$ for $x_2 > K_2$.
- (C3) $h_2(x_2, 0) < 0$ for $x < A_2$, $h_2(x_2, 0) > 0$ for $A_2 < x_2 < K_2$ and $h_2(x_2, 0) < 0$ for $x > K_2$.
- (C4) For any $x_1 > 0$ there is $K_{x_1} > 0$ such that $h_2(x_2, x_1) < 0$ for all $x_2 > K_{x_1}$.
- (M) $h_2(x_2, x_1)$ is continuously differentiable and increasing in x_1,

$$\frac{\partial h_2}{\partial x_1}(x_2, x_1) > 0.$$

Assumption (C1) ensures that all solutions of the first equation are bounded and any given solution x_1 converges to an equilibrium point, which is either 0 or a root of $h_1(x_1) = 0$. Assumption (C2), formulated for the second species, is similar to (C1), stating also that this species is not subject to a strong Allee effect. Assumption (C3), dual to (C2), states that the second species is subject to a strong Allee effect in the absence of commensalism.

Assumption (C4) ensures that the effects of commensalism do not lead to unbounded growth for the benefitting species, irrespective of the population size of the other one. Finally, assumption (M) states that the model (7.9) describes indeed a commensalism, since increasing the population of the first species has a beneficial effect upon the growth of the second one.

Let x_1^* be an equilibrium of the first equation and let x_1 be a solution such that $x_1(t) \to x_1^*$ as $t \to \infty$. Using the mean value theorem and assumption (M), it follows that h_2 is locally Lipschitz as a function of x_1 and consequently

$$|h_2(x_2, x_1) - h_2(x_2, x_1^*)| < B|x_1 - x_1^*|,$$

where B is a constant that depends only on the compact set containing x_1 and x_2. Hence $h_2(x_2, x_1)$ converges locally uniformly to $h_2\big(x_2, x_1^*\big)$. From this, we can consider x_2 as described by an asymptotically autonomous differential equation

$$x_2' = r_2 x_2 h_2(x_2, x_1), \tag{7.10}$$

with limiting equation given by

$$x_2' = r_2 x_2 h_2\big(x_2, x_1^*\big). \tag{7.11}$$

Our main result is given as follows.

Theorem 7.4. *Suppose* (C1), (C2), (C4) *and* (M) *hold for* (7.9) *and that for each locally stable equilibrium* x_1^* *of the first equation of* (7.9) *there exists a unique equilibrium* x_2^* *of* (7.11). *If* $x_1(t) \to x_1^*$ *then* $x_2(t) \to x_2^*$ *for any* $x_2(0) > 0$.

Before presenting the proof, note that we did not assume that x_1^* is unique because this restriction is not necessary.

Proof. Notice that, by (M), $h_2\big(0, x_1^*\big) > h_2(0,0) \geq 0$. Also, from (C4), $h_2\big(x_2, x_1^*\big)$ is eventually negative. Hence, if x_2^* is unique, it is automatically a globally stable equilibrium for the limiting equation (7.11).

We now verify the conditions of Theorem 7.2. Consider $X_1 = \{0\}$ and $X_2 = (0, \infty)$. Notice that X_1 is closed, X_2 is open and they form a disjoint partition of $[0, \infty)$, the solution space of (7.11). Furthermore, 0 is a weak repeller for (7.10) since if $x_2 \to 0$ for $x_2(0) > 0$ then we would have

$$\frac{x_2'}{x_2} = r_2 h_2(x_2, x_1) > r_2 h_2(x_2, 0) \to r_2 h_2(0,0) \geq 0.$$

Therefore the basin of attraction of x_2^* in (7.10) and (7.11) is the same and $x_2(t) \to x_2^*$ in (7.9). □

If we assume a strong Allee effect for x_2, that is, we replace assumption (C2) with assumption (C3), we see that a necessary and sufficient condition to prevent species x_2 extinction is

$$h_2\big(0, x_1^*\big) > 0.$$

This ensures that 0 is always a repeller for x_2. If this condition holds, the previous theorem remains unchanged. However if $h_2\big(0, x_1^*\big) < 0$, then there will always be a strong Allee threshold for x_2, albeit one smaller than A_2 due to the commensalistic effect. In addition, there will always be at least two positive equilibria for x_2 corresponding to every x_1^*. Then, from Theorem 7.1 we have that each solution of (7.10) will converge to an equilibrium of (7.11) but, again, without the preservation of the basins of attraction.

8. Conclusions

In this paper, we analyzed from a stability viewpoint several models of two-species commensalisms, which represent biological interactions in which only one species benefits while the other is left unaffected. In particular, we chose models with Richards and restricted growth rate, respectively, which are the commensalistic equivalents of the mutualistic models analyzed in [9]. With several modifications made following an unitary procedure defined *ad hoc*, we showed that the Lyapunov functionals employed in [8, 9] can be extended to prove global stability theorems of the corresponding commensalistic models.

This extends the area of usefulness of these functionals in tackling stability problems. This is particularly important for modeling problems since, on one hand, global stability results give confidence to their biological interpretation but, on the other hand, there is no universal mathematical algorithm to establish global stability for all models enjoying this property. As an added benefit, these stability results, within the context of commensalism, may be used to approximate the behavior of two-species interaction in which one has only a negligible effect on the other.

Incorporating an Allee effect in the intrinsic growth rate of the positively influenced species, we have also investigated in the second part of the paper how a commensalistic interaction prevents or maintains the possibility of population decline or extinction. To this purpose, we have employed the theory of asymptotically autonomous systems.

From a biological perspective, both above-mentioned outcomes can be important. For example a commensalistic species can be introduced to prevent the extinction of an endangered species. In this regard, it has been observed in [12] that although positive interactions, in which one species benefits from the presence of another species, such as mutualisms and commensalisms, are not usually well integrated into contemporary approaches to aquatic restoration and conservation, they can often initiate recruitment and facilitation cascades which promote an enhanced reproductive success. Further, positive interactions can be conducted among populations and species across a wide range of scales (see [12, Table 1]), since resources are often transferred between ecosystems via species migration and the transport of organic nutrients. To this purpose, the spatial arrangement, the connection between ecosystems, needs to be explicitly accounted for, in order for the restoration of an ecosystem to be used to promote the enhancement of others.

On the other hand, the interaction between humans and invasive species (accidentally and/or intentionally introduced in a habitat) can be modeled by a commensalistic interaction (human and invasive species) in which the invasive species benefits from human actions. In such a case extinction may be desirable to prevent the invasive species from establishing itself [4].

A more comprehensive research that addresses these problems from an unifying abstract viewpoint is currently underway and it will be reported in a forthcoming paper.

Acknowledgments

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. D. Maxin acknowledges funding from Wheat Ridge Ministries — O. P. Kretzmann Grant for Research in the Healing Arts and Sciences. The work of H. Zhang was supported by the National Natural Science Foundation of China, Grant ID 11201187, the Scientific Research Foundation for the Returned Overseas Chinese Scholars and the China Scholarship Council.

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