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Global stability of the coexistence equilibrium for a general class of models of facultative mutualism

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ABSTRACT

Many models of mutualism have been proposed and studied individually. In this paper, we develop a general class of models of facultative mutualism that covers many of such published models. Using mild assumptions on the growth and self-limiting functions, we establish necessary and sufficient conditions on the boundedness of model solutions and prove the global stability of a unique coexistence equilibrium whenever it exists. These results allow for a greater flexibility in the way each mutualist species can be modelled and avoid the need to analyse any single model of mutualism in isolation. Our generalization also allows each of the mutualists to be subject to a weak Allee effect. Moreover, we find that if one of the interacting species is subject to a strong Allee effect, then the mutualism can overcome it and cause a unique coexistence equilibrium to be globally stable.

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1. Introduction

A mutualism is an interaction between a pair of species that is beneficial for both parties and that is commonly manifested as an increase in an individual's capacity to grow, survive or reproduce [16]. Mutualisms are many and varied [18], including associations between pollinators and plants [31], seed dispersers and plants [26], mycorrhizae and plants [23], and cleaner species and their hosts [9]. By degree of dependency, a mutualist can be classified as facultative when it benefits from the interaction yet can survive on its own, or obligate when it requires an interaction as it is not able to survive without the other species. Moreover, mutualisms can be protective when a species gets physical protection by the other species (such as when clown fish hide in sea anemones) or resource-based when a species receives a resource (such as when bees collect nectar). Most likely, it is because of this diversity and complexity of mutualistic interactions that work on predatory and competitive interactions has always dominated in ecology.

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A number of mathematical models have been proposed to describe mutualistic interactions, starting with the familiar Lotka–Volterra model [31]. It is a legacy of this pioneering mutualism model that a majority of its successors focus on facultative mutualisms, are composed of two structurally identical equations and aim to prevent populations from increasing without bounds as a result of reinforcing effects of their mutual benefits [17, 18, 31]. Once a stable coexistence equilibrium is shown to exist, a mathematical question of biological interest that typically follows is establishing its uniqueness and/or global stability. As one may imagine, looking for uniqueness and/or global stability of a coexistence equilibrium in a mutualism model (but also in any other similarly complex model) is a difficult task.

The high diversity of mutualistic interactions calls for a similar diversity of mathematical models [17, 18, 31]. For instance, the Lotka–Volterra mutualism model represents the situation in which the per capita effects of a (facultative) mutualism are density independent

$$\begin{aligned}x'_1 &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \frac{r_1 b_{12}}{K_1} x_1 x_2 = r_1 x_1 \left(1 + \frac{b_{12} x_2}{K_1} - \frac{x_1}{K_1}\right), \\x'_2 &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \frac{r_2 b_{21}}{K_2} x_1 x_2 = r_2 x_2 \left(1 + \frac{b_{21} x_1}{K_2} - \frac{x_2}{K_2}\right).\end{aligned}\tag{1}$$

On the contrary, Wolin and Lawlor [32] introduced the following model to accommodate the situation in which a (facultative) mutualism has a higher per capita impact at higher densities

$$\begin{aligned}x'_1 &= r_1 x_1 - \frac{r_1 x_1^2}{K_1 + b_{12} x_2} = r_1 x_1 \left(1 - \frac{x_1}{K_1 + b_{12} x_2}\right), \\x'_2 &= r_2 x_2 - \frac{r_2 x_2^2}{K_2 + b_{21} x_1} = r_2 x_2 \left(1 - \frac{x_2}{K_2 + b_{21} x_1}\right).\end{aligned}\tag{2}$$

In both models (1) and (2), r_i is the intrinsic growth rate and K_i is the carrying capacity of species, $i=1,2$ when alone. In addition, b_{12} and b_{21} are positive constants that scale the beneficial effect of one species on the other. Hence, if one species is missing, the other grows in a logistic fashion. However, the mutualistic association is manifested differently in models (1) and (2), which translates into different signs of the interaction terms. In particular, while model (1) is a special case of a general model

$$\begin{aligned}x'_1 &= r_1 x_1 [f_1(x_1, x_2) - a_1(x_1)], \\x'_2 &= r_2 x_2 [f_2(x_2, x_1) - a_2(x_2)]\end{aligned}\tag{3}$$

for some positive functions a_1, a_2, f_1, f_2 , model (2) can rather be generalized as

$$\begin{aligned}x'_1 &= r_1 x_1 [a_1(x_1) - f_1(x_1, x_2)], \\x'_2 &= r_2 x_2 [a_2(x_2) - f_2(x_2, x_1)].\end{aligned}\tag{4}$$

It would certainly be a good move if the issues of uniqueness and/or global stability of a coexistence equilibrium were resolved for some general classes of models of mutualism such as these.

In this direction, Georgescu and Zhang [12] formulated sufficient conditions for the global stability of a unique coexistence equilibrium for a general model of mutualism, in the form

$$\begin{aligned}x_1' &= a_1(x_1) + f_1(x_1)g_1(x_2), \\x_2' &= a_2(x_2) + f_2(x_2)g_2(x_1),\end{aligned}\tag{5}$$

under various trade-offs between monotonicity and sign conditions of the (not necessarily positive) functions $a_1, a_2, f_1, f_2, g_1, g_2$ and their combinations. Note that model (5) also includes models (1) and (2) as its special cases. Lyapunov functionals extending those of [30] were used to explore global stability in this case. Georgescu et al. [13] further enlarged applicability of the abstract functionals introduced in [12] to a model of mutualism with restricted growth rates proposed in [14] and to the versions of models (1) and (2) with the logistic growth rates replaced by the Richards ones.

Despite a variety of proposed models of mutualism, there is still potential for developing others. As we have already emphasized above, most models of mutualism assume a symmetry of the interaction effect. That is, the mutualistic effect is commonly modelled using structurally identical equations [17, 18, 31], as is also exemplified by models (1) and (2). Although this may suffice for certain systems, in other cases the mutualists have different life histories, such as when representing a plant and an animal [31]. Not only may interaction terms differ structurally for each mutualist, but also beneficial effects of mutualism may impact different fitness components in each species. For instance, in the sea anemone–anemone fish mutualism, waste ammonia from the fish feed the symbiotic algae that are found in the anemone's tentacles [22]. Similarly, by consuming parasitic bugs on the zebras' or rhinos' skin, the oxpeckers acquire food and the zebras or rhinos get rid of pests [4]. Last but not least, the spider crabs prefer shallow waters and seek algae that would grow on their back. This way the crabs are camouflaged and thus more likely to escape predation, while the algae obtain an extra resource which is another place to live at [4]. Of course, the same fitness component may be affected in both mutualists, such as in the case of brood-site pollination mutualism [25] or when some ants nest inside thorns of trees of the genus *Acacia*; in exchange for shelter, the ants protect acacias from attack by herbivores [15]. Therefore, any sufficiently general class of mutualism models should also allow for equations that are structurally different and cover cases in which different fitness components are affected in different species.

Apart from some exceptions such as [21], all published models of mutualism assume that individual species grow in a logistic manner when alone. In the recent decades, however, biologists have started to acknowledge that populations may be subject to an Allee effect, a concept originally studied by Allee [1, 2]. Allee effects occur when mean individual fitness declines with decreasing population density when the population is rare and can occur due to a plethora of causes, the most prominent being enhanced difficulties of individuals to find mates, escape predation or avoid inbreeding when population densities become low [6, 7, 11, 29].

Allee effects can be classified as weak or strong. In both cases, the per capita population growth rate declines with decreasing population density when the population is rare. Weak Allee effects occur when, despite this decline, the per capita growth rate never becomes negative in low-density populations [6, 29]. As with the logistic growth, populations always

attain the carrying capacity, yet at a slower rate when rare. On the other hand, strong Allee effects occur when the per capita growth rate becomes negative once the population density falls below a critical value termed an Allee threshold [6, 29]. Populations above the Allee threshold attain the carrying capacity, while those below the Allee threshold go extinct. For instance, the population model

$$x' = rx \left(\frac{x}{A} - 1 \right) \left(1 - \frac{x}{K} \right), \quad 0 < A < K, \quad (6)$$

exhibits a strong Allee effect with the Allee threshold A ; populations with densities below A go extinct, while those above A attain the carrying capacity K . An example of a model with a weak Allee effect is provided by the following modification of the classical logistic model:

$$x' = rx^p \left(1 - \frac{x}{K} \right), \quad p > 1. \quad (7)$$

For $p > 1$, the per capita growth rate $f(x) = rx^{p-1}(1 - x/K)$ is indeed positive and increasing at small densities. Since there is no Allee threshold in this model, the Allee effect is weak. If $p = 1$, the model (7) represents the classical logistic equation. Other single-species models of Allee effects have been proposed in [6, 8, 24].

An important role of mutualistic models such as the Lotka–Volterra one and many of its successors is to propose generalizations that hold for many specific mutualistic interactions. Ability to establish uniqueness and/or global stability of a coexistence equilibrium for a general class of mutualism models is certainly a decent step in this direction. The aim of this article is thus twofold. First, we propose a general class of models of facultative mutualism that covers a broad set of existing mutualistic models, including Equations (1) and (2), and allows for asymmetry of the mutual species effect (i.e. mutualistic effects need not be modelled in the same way for each species) and/or populations subject to some Allee effects. Second, we provide mathematical proofs for this class of models concerning the boundedness of their solutions and the global stability of the unique coexistence equilibrium whenever it exists.

The paper is organized as follows. In Section 2, we propose our general class of facultative models of mutualism and prove our main theoretical results. In Section 3, we provide several biologically motivated examples to illustrate how our general results may apply to specific models of mutualism. A discussion on the biological implications of our results as well as on future research avenues is given in Section 4.

2. The general model

Before developing and analysing the models of mutualism, we first introduce a single-species model which describes the dynamics of a species in the absence of mutualism. We assume that the dynamics of each species in isolation is modelled as

$$x' = rx[a(x) - f(x)], \quad (8)$$

where a and f are positive real-valued continuous functions, which shall be elaborated upon later on. In what follows, a is to be interpreted as a growth function, and f as a self-limiting function. We now introduce the following *growth assumption*:

- (G) There exists $K > 0$ such that $a(x) - f(x) > 0$ for $x < K$, $a(x) - f(x) < 0$ for $x > K$ and $a(K) - f(K) = 0$.

This ensures that the population approaches the carrying capacity K from every positive initial density, and therefore covers both logistic-like population dynamics and dynamics of a population subject to a weak Allee effect. This assumption will be modified later on when treating strong Allee effects in mutualistic interactions.

2.1. Mutualisms that affect the self-limiting function

Let us now consider the following abstract model of a mutualistic interaction:

$$\begin{aligned}x'_1 &= r_1 x_1 [a_1(x_1) - f_1(x_1, x_2)], \\x'_2 &= r_2 x_2 [a_2(x_2) - f_2(x_2, x_1)],\end{aligned}\tag{9}$$

in which $r_1, r_2 > 0$, a_1, a_2 are positive functions continuously differentiable on \mathbb{R} and f_1, f_2 are positive functions continuously differentiable on \mathbb{R}^2 . We shall also assume that the expressions $a_1(x_1) - f_1(x_1, 0)$ and $a_2(x_2) - f_2(x_2, 0)$ satisfy the growth assumption (G) with K_1 and K_2 as the respective single-species carrying capacities.

We now introduce the following *consistency assumptions*:

- (C1) $f_1(x_1, x_2)$ is increasing in x_1 and $f_2(x_2, x_1)$ is increasing in x_2 .
(C2) $a_1(x_1)/f_1(x_1, x_2)$ is strictly decreasing in x_1 and $a_2(x_2)/f_2(x_2, x_1)$ is strictly decreasing in x_2 .
(C3) $a_1(x_1)/f_1(x_1, \alpha x_1)$ and $a_2(x_2)/f_2(x_2, \alpha x_2)$ are eventually decreasing for all $\alpha > 0$.
That is,

$$\begin{aligned}\frac{d}{dx_1} \left(\frac{a_1(x_1)}{f_1(x_1, \alpha x_1)} \right) &< 0 \quad \text{for } x_1 > M_1, \\ \frac{d}{dx_2} \left(\frac{a_2(x_2)}{f_2(x_2, \alpha x_2)} \right) &< 0 \quad \text{for } x_2 > M_2,\end{aligned}$$

where M_1 and M_2 are positive real numbers that may depend on α .

The common meaning of the assumptions (C1) and (C2) is that if one species is kept constant, then the other should still follow a logistic-like or weak Allee effect growth in which the ratio between the growth and self-limiting functions decreases as the population density increases. The meaning of (C3) is somewhat similar, supposing this time that the ratio between the population densities is kept constant. In particular, the assumption (C3) has intentionally a weaker monotonicity property which allows our boundedness theorems formulated and proved below to hold also for mutualism models including strong Allee effects.

We now define the *mutualism-specific assumption*:

(M) $f_1(x_1, x_2)$ is decreasing in x_2 and $f_2(x_2, x_1)$ is decreasing in x_1 .

Noting that f_1 and f_2 appear with negative signs in the model (9), the assumption (M) characterizes the fact that the model (9) indeed represents a mutualistic interaction, since an increase in the density of a population benefits the other species, for all population densities.

Due to the assumption (C3), for all $\alpha > 0$ there exist finite non-negative numbers $\mathcal{R}_1(\alpha)$, $\mathcal{R}_2(\alpha)$ given by

$$\mathcal{R}_1(\alpha) = \lim_{x_1 \rightarrow \infty} \frac{a_1(x_1)}{f_1(x_1, \alpha x_1)}, \quad \mathcal{R}_2(\alpha) = \lim_{x_2 \rightarrow \infty} \frac{a_2(x_2)}{f_2(x_2, \alpha x_2)}.$$

Due to the assumption (M), \mathcal{R}_1 , \mathcal{R}_2 are increasing as functions of α , although they may not necessarily be strictly increasing (it shall be observed later on that one or both of them may even be identically 0). Also, by the assumption (G), $\mathcal{R}_1(0) < 1$ and $\mathcal{R}_2(0) < 1$.

The existence of a coexistence equilibrium \mathbf{E}^* of the model (9) can be characterized in terms of a joint quantitative property of \mathcal{R}_1 and \mathcal{R}_2 , as follows.

Lemma 2.1: *If the assumption (C3) holds for all positive x_1 and x_2 and there exists a coexistence equilibrium \mathbf{E}^* of the model (9), then there is $\alpha > 0$ such that $\mathcal{R}_1(\alpha) < 1$ and $\mathcal{R}_2(1/\alpha) < 1$.*

Proof: Let $\mathbf{E}^* = (x_1^*, x_2^*)$ be a coexistence equilibrium of the model (9). Because of that

$$\frac{a_1(x_1^*)}{f_1(x_1^*, x_2^*)} = 1, \quad \frac{a_2(x_2^*)}{f_2(x_2^*, x_1^*)} = 1.$$

Denoting $\alpha = x_2^*/x_1^*$, this yields

$$\frac{a_1(x_1^*)}{f_1(x_1^*, \alpha x_1^*)} = 1, \quad \frac{a_2(x_2^*)}{f_2(x_2^*, \frac{1}{\alpha} x_2^*)} = 1,$$

and the conclusion follows using the assumption (C3). ■

This result suggests a characterization of whether solutions of the model (9) are bounded through conditions imposed on \mathcal{R}_1 and \mathcal{R}_2 . We first establish the boundedness of solutions of the model (9).

Theorem 2.2: *Let the assumptions (C1) and (C3) hold. If there is $\alpha > 0$ such that $\mathcal{R}_1(\alpha) < 1$ and $\mathcal{R}_2(1/\alpha) < 1$, then solutions of the model (9) are uniformly bounded in a compact region of the positive quadrant and there is a coexistence equilibrium \mathbf{E}^* .*

Proof: First, we shall prove that any solution that starts with positive initial conditions will not have a limit point on any of the semi-axes. Due to (M) and (G), it follows that

$$x_1' > r_1 x_1 [a_1(x_1) - f_1(x_1, 0)] > 0, \quad x_2' > r_2 x_2 [a_2(x_2) - f_2(x_2, 0)] > 0$$

provided that x_1, x_2 stay positive and under their corresponding carrying capacities. Consequently, solutions starting with positive initial conditions cannot get too close to any of the positive semi-axes and the system (9) is uniformly persistent.

To show that the solutions are bounded from above, we consider the function

$$h(t) = \max\{\alpha x_1(t), x_2(t)\}.$$

For a given $t > 0$, we have two possibilities.

Case 1. $h(t) = \alpha x_1(t)$. Then $x_2(t) \leq \alpha x_1(t)$ and, due to (M)

$$\frac{x_1'}{x_1} \leq r_1 f_1(x_1, \alpha x_1) \left[\frac{a_1(x_1)}{f_1(x_1, \alpha x_1)} - 1 \right].$$

Since the expression inside the square brackets has limit $\mathcal{R}_1(\alpha) - 1 < 0$, it follows that $x_1'/x_1 < 0$ for x_1 large enough, say for $x_1 > M_1$.

Case 2. $h(t) = x_2(t)$. Then $x_1(t) \leq (1/\alpha)x_2(t)$ and, due to (M)

$$\frac{x_2'}{x_2} \leq r_2 f_2\left(x_2, \frac{1}{\alpha}x_2\right) \left[\frac{a_2(x_2)}{f_2(x_2, \frac{1}{\alpha}x_2)} - 1 \right].$$

Again, since the expression inside the square brackets has limit $\mathcal{R}_2(1/\alpha) - 1 < 0$, it follows that $x_2'/x_2 < 0$ for x_2 large enough, say for $x_2 > M_2$.

Even though αx_1 and x_2 are differentiable, the function h may not necessarily be so for all $t > 0$ (it is, however, continuous for all $t \geq 0$). Specifically, h may not be differentiable for values of t such that $hx_1(t) = x_2(t)$. However, the following result [20, Lemma 1.2.1] provides a condition for the monotonicity of continuous functions using only Dini derivatives.

Lemma 2.3: *Suppose that $u \in C([t_0, t_0 + a], \mathbb{R})$ and the inequality $Du(t) \leq 0$ holds for $t \in [t_0, t_0 + a] \setminus S$, D being any Dini derivative and S being an at most countable subset of $[t_0, t_0 + a]$. Then $u(t)$ is nonincreasing in t on $[t_0, t_0 + a]$.*

From the above discussion, it is seen that

$$D^+h(t) < 0, \quad \text{whenever } h(t) > M := \max\{\alpha M_1, M_2\},$$

where $D^+h(t)$ is the upper right Dini derivative of h , defined as

$$D^+h(t) = \limsup_{\epsilon \rightarrow 0^+} \frac{h(t + \epsilon) - h(t)}{\epsilon}.$$

Consequently, h is uniformly bounded from above. Since $h(t) := \max\{\alpha x_1(t), x_2(t)\}$, it follows that x_1 and x_2 are also uniformly bounded from above. Moreover, all solutions starting in the positive quadrant eventually enter the compact region of this quadrant defined by $\max\{\alpha x_1, x_2\} \leq \max\{\alpha M_1, M_2\}$ regardless of initial population densities.

Finally, by Theorem 2.8.6 of Bhatia and Szegő [3] (see also [28], Theorem D.3), there is a coexistence equilibrium E^* . ■

A well-known sufficient condition to rule out the existence of periodic orbits of a dynamical system in a simply connected region of the plane is given in the following theorem.

Theorem 2.4 (Dulac criterion): *Let D be an open and simply connected region of the plane and consider the dynamical system given by*

$$\begin{aligned}x'_1 &= f(x_1, x_2), \\x'_2 &= g(x_1, x_2).\end{aligned}\tag{10}$$

Let the functions f and g be continuously differentiable on D and suppose that there is a continuously differentiable function φ on D (called a Dulac function) such that $(\partial/\partial x_1)(\varphi f) + (\partial/\partial x_2)(\varphi g)$ is either strictly positive or strictly negative almost everywhere on D . Then D does not contain any periodic solution of system (10).

We are now able to state and prove our stability result concerning a coexistence equilibrium.

Theorem 2.5: *Suppose that the assumptions (C1), (C2), (C3) hold, there is $\alpha > 0$ such that $\mathcal{R}_1(\alpha) < 1$ and $\mathcal{R}_2(1/\alpha) < 1$ and there is a unique coexistence equilibrium \mathbf{E}^* . Then \mathbf{E}^* is globally asymptotically stable.*

Proof: Under the assumptions of this theorem, the global stability of \mathbf{E}^* follows from ruling out periodic solutions using the Dulac criterion with the following Dulac function

$$\varphi(x_1, x_2) := \frac{1}{x_1 x_2 a_1(x_1) a_2(x_2)}.$$

Using assumption (C2), the differential expression appearing in the Dulac criterion evaluates as

$$\begin{aligned}&\frac{\partial}{\partial x_1}[\varphi(x_1, x_2)x'_1] + \frac{\partial}{\partial x_2}[\varphi(x_1, x_2)x'_2] \\&= -\frac{r_1}{x_2 a_2(x_2)} \frac{\partial}{\partial x_1} \left[\frac{f_1(x_1, x_2)}{a_1(x_1)} \right] - \frac{r_2}{x_1 a_1(x_1)} \frac{\partial}{\partial x_2} \left[\frac{f_2(x_2, x_1)}{a_2(x_2)} \right] < 0.\end{aligned}$$

Therefore, no periodic solution exists in the first quadrant for the model (9) and \mathbf{E}^* is thus globally asymptotically stable.

Note also that if the assumption (C3) holds for all positive x_1 and x_2 , the existence of a unique coexistence equilibrium \mathbf{E}^* implies that all solutions of the model (9) are uniformly bounded, by Lemma 2.1 and Theorem 2.2. ■

Remark 2.1: In some sense, α is a critical ratio, although in this context one may find a continuum of critical ratios rather than a single one. If the ratio between densities of the second and first species equals α , both species experience a decrease at large population densities, since negative rates surpass positive ones. If this ratio falls below α , to some $\beta < \alpha$, then, due to the monotonicity of \mathcal{R}_1 , the first species, which is now ‘excedentary’, will have to decrease its density, since $\mathcal{R}_1(\beta) \leq \mathcal{R}_1(\alpha) < 1$. Similarly, if this ratio goes above α , to some $\gamma > \alpha$, then due to the monotonicity of \mathcal{R}_2 , it will be the turn of the second species to be ‘excedentary’ and to decrease its density, since $\mathcal{R}_2(1/\gamma) \leq \mathcal{R}_2(1/\alpha) < 1$. That is, the inequalities $\mathcal{R}_1(\alpha) < 1$ and $\mathcal{R}_2(1/\alpha) < 1$ help create a balance mechanism, which keeps unboundedness in check.

The following result shows that the boundedness condition from the previous theorem is necessary to guarantee that all solutions are bounded (and thus to avoid the unrealistic reinforcing of the mutualistic effects).

Theorem 2.6: *Let the assumptions (C1) and (C3) hold. If there is $\alpha > 0$ such that $\mathcal{R}_1(\alpha) > 1$ and $\mathcal{R}_2(1/\alpha) > 1$, then solutions of the model (9) are unbounded if the initial population density is large enough.*

Proof: We have already seen that solutions of the model (9) are bounded from below by a strictly positive constant. Hence we can assume that there exists $\xi > 0$ such that $x_1(t) > \xi$ and $x_2(t) > \xi$. Seeking for a contradiction, we assume that the function

$$h(t) := \min\{\alpha x_1(t), x_2(t)\}$$

is bounded from above, i.e. $h(t) < M$ for a certain $M > 0$ and for any t . With these assumptions we have the following two cases for each $t > 0$.

Case 1. $h(t) = \alpha x_1(t)$. One then has, by (M) and the first part of (C1)

$$\begin{aligned} \frac{x_1'}{x_1} &\geq r_1[a_1(x_1) - f_1(x_1, \alpha x_1)] = r_1 f_1(x_1, \alpha x_1) \left[\frac{a_1(x_1)}{f_1(x_1, \alpha x_1)} - 1 \right] \\ &> r_1 f_1(\xi, M) \left[\frac{a_1(x_1)}{f_1(x_1, \alpha x_1)} - 1 \right]. \end{aligned}$$

Assuming that $x_1(0) > M_1 > 0$ the last term is positive and decreasing in x_1 . Passing to the limit as $x_1 \rightarrow \infty$ and using (C3), it follows that

$$\frac{x_1'}{x_1} > r_1 f_1(\xi, M) [\mathcal{R}_1(\alpha) - 1] > 0.$$

Case 2. $h(t) = x_2(t)$. One then has, again by (M) and the first part of (C1), that

$$\begin{aligned} \frac{x_2'}{x_2} &\geq r_1 \left[a_2(x_2) - f_2 \left(x_2, \frac{1}{\alpha} x_2 \right) \right] = r_2 f_2 \left(x_2, \frac{1}{\alpha} x_2 \right) \left[\frac{a_2(x_2)}{f_2(x_2, \frac{1}{\alpha} x_2)} - 1 \right] \\ &> r_2 f_2 \left(\xi, \frac{M}{\alpha} \right) \left[\frac{a_2(x_2)}{f_2(x_2, \frac{1}{\alpha} x_2)} - 1 \right]. \end{aligned}$$

Similarly, if $x_2(0) > M_2 > 0$, passing to the limit as $x_2 \rightarrow \infty$ in the last term and using (C3), it follows that

$$\frac{x_2'}{x_2} > r_2 f_2 \left(\xi, \frac{M}{\alpha} \right) \left[\mathcal{R}_2 \left(\frac{1}{\alpha} \right) - 1 \right] > 0.$$

This shows that h'/h is bounded from below by a strictly positive constant $C > 0$ with

$$C := \min \left\{ r_1 f_1(\xi, M) [\mathcal{R}_1(\alpha) - 1], r_2 f_2 \left(\xi, \frac{M}{\alpha} \right) \left[\mathcal{R}_2 \left(\frac{1}{\alpha} \right) - 1 \right] \right\} > 0,$$

as long as $h(0) > \max\{\alpha M_1, M_2\}$. While h' is not differentiable everywhere in the classical sense, as an increasing function it is differentiable almost everywhere and the following

weak version of the Fundamental Theorem of Calculus holds

$$\int_0^t \frac{h'(\tau)}{h(\tau)} d\tau \leq \ln h(t) - \ln h(0).$$

We thus have

$$\ln h(t) - \ln h(0) \geq \int_0^t \frac{h'(\tau)}{h(\tau)} d\tau > \int_0^t C d\tau = Ct.$$

Letting $t \rightarrow \infty$ in this inequality, it follows that $h(t) \rightarrow \infty$. This contradicts the assumption that h is bounded from above. Hence h and, therefore, both x_1 and x_2 are unbounded. ■

Remark 2.2: It can be seen that the conditions for boundedness and unboundedness are mutually exclusive. To this purpose, note that, since \mathcal{R}_1 and \mathcal{R}_2 are increasing

$$[\mathcal{R}_1(\alpha) - \mathcal{R}_1(\beta)] \left[\mathcal{R}_2\left(\frac{1}{\alpha}\right) - \mathcal{R}_2\left(\frac{1}{\beta}\right) \right] \leq 0 \quad \text{for all } \alpha, \beta \geq 0.$$

Consequently, if there is any α such that $\mathcal{R}_1(\alpha) < 1$ and $\mathcal{R}_2(1/\alpha) < 1$, there cannot be any β such that $\mathcal{R}_1(\beta) > 1$ and $\mathcal{R}_2(1/\beta) > 1$, and vice versa.

Remark 2.3: The boundedness conditions derived in our theorems can be expressed in the form of a single threshold for a broad class of mutualism models, including most of the models already analysed in the literature. For example, this is always the case when the limits $\mathcal{R}_1(\alpha)$ and $\mathcal{R}_2(\alpha)$ come from rational expressions, having the form

$$\mathcal{R}_1(\alpha) = C_1 \alpha^{p_1}, \quad \mathcal{R}_2(\alpha) = C_2 \alpha^{p_2}, \quad p_1, p_2 > 0, \quad C_1, C_2 \geq 0. \quad (11)$$

Then the boundedness condition is equivalent to finding $\alpha > 0$ such that

$$C_1 \alpha^{p_1} < 1, \quad C_2 \left(\frac{1}{\alpha} \right)^{p_2} < 1.$$

If one of the constants C_1, C_2 is 0, then the boundedness condition is satisfied regardless of the value of the other constant. For example, if $C_1 = 0$ then $\mathcal{R}_1(\alpha) = 0$ for any α and $\mathcal{R}_2(1/\alpha)$ can be made less than 1 by choosing α large enough. Similarly, if $C_2 = 0$ then $\mathcal{R}_2(1/\alpha)$ is always zero and $\mathcal{R}_1(\alpha)$ can be made less than 1 by choosing α small enough. If both \mathcal{R}_1 and \mathcal{R}_2 are identically zero, then the boundedness follows without any condition on the existence of a suitable α .

Finally, if $C_1, C_2 > 0$, then

$$C_1 \alpha^{p_1} < 1, \quad C_2 \left(\frac{1}{\alpha} \right)^{p_2} < 1 \implies C_2^{1/p_2} < \alpha < \left(\frac{1}{C_1} \right)^{1/p_1},$$

condition which is satisfied if $C_1^{1/p_1} C_2^{1/p_2} < 1$. It follows that the boundedness condition is satisfied for all values of C_1, C_2 , null or not, such that $C_1^{1/p_1} C_2^{1/p_2} < 1$.

Similarly, the unboundedness condition is equivalent to finding $\alpha > 0$ such that

$$C_1 \alpha^{p_1} > 1, \quad C_2 \left(\frac{1}{\alpha} \right)^{p_2} > 1.$$

Obviously, the unboundedness condition cannot be satisfied if any of C_1, C_2 is null. If $C_1, C_2 > 0$, then

$$C_1 \alpha^{p_1} > 1, \quad C_2 \left(\frac{1}{\alpha} \right)^{p_2} > 1 \implies \left(\frac{1}{C_1} \right)^{1/p_1} < \alpha < C_2^{1/p_2},$$

condition which is satisfied if $C_1^{1/p_1} C_2^{1/p_2} > 1$.

Consequently, in the particular case defined by Equation (11), our conditions are threshold-like. Specifically, if we define

$$\mathcal{R} = C_1^{1/p_1} C_2^{1/p_2}, \quad (12)$$

then the boundedness condition can be expressed as $\mathcal{R} < 1$, while the unboundedness condition can be expressed as $\mathcal{R} > 1$.

2.2. Mutualisms that affect the growth function

We now show that the approach used to discuss stability of Equation (9) can be easily adapted for the situation in which the mutualism affects the growth function a rather than the self-limiting function f . The main theorems presented above still hold and, since their proofs are very similar, we only state here the specific assumptions, thresholds and the Dulac function to be used in the argument for non-existence of periodic solutions.

$$\begin{aligned} x_1' &= r_1 x_1 [f_1(x_1, x_2) - a_1(x_1)], \\ x_2' &= r_2 x_2 [f_2(x_2, x_1) - a_2(x_2)]. \end{aligned} \quad (13)$$

The *consistency assumptions* are now as follows:

- (C1) $a_1(x_1)$ is increasing in x_1 and $a_2(x_2)$ is increasing in x_2 ,
- (C2) $f_1(x_1, x_2)/a_1(x_1)$ is decreasing in x_1 and $f_2(x_2, x_1)/a_2(x_2)$ is decreasing in x_2 ,
- (C3) $f_1(x_1, \alpha x_1)/a_1(x_1)$ and $f_2(x_2, \alpha x_2)/a_2(x_2)$ are eventually decreasing for all $\alpha > 0$,

and the *mutualism-specific assumption* is

- (M) $f_1(x_1, x_2)$ is increasing in x_2 and $f_2(x_2, x_1)$ is increasing in x_1 .

Hence, the limits $\mathcal{R}_1(\alpha), \mathcal{R}_2(\alpha)$ are now given by

$$\mathcal{R}_1(\alpha) = \lim_{x_1 \rightarrow \infty} \frac{f_1(x_1, \alpha x_1)}{a_1(x_1)}, \quad \mathcal{R}_2(\alpha) = \lim_{x_2 \rightarrow \infty} \frac{f_2(\alpha x_2, x_2)}{a_2(x_2)},$$

and the Dulac function corresponding to the model (13) is $\varphi(x_1, x_2) := 1/x_1 x_2 a_1(x_1) a_2(x_2)$, which leads to

$$\begin{aligned} & \frac{\partial}{\partial x_1} [\varphi(x_1, x_2) x'_1] + \frac{\partial}{\partial x_2} [\varphi(x_1, x_2) x'_2] \\ &= \frac{r_1}{x_2 a_2(x_2)} \frac{\partial}{\partial x_1} \left[\frac{f_1(x_1, x_2)}{a_1(x_1)} \right] + \frac{r_2}{x_1 a_1(x_1)} \frac{\partial}{\partial x_2} \left[\frac{f_2(x_2, x_1)}{a_2(x_2)} \right] < 0 \end{aligned}$$

for any positive x_1 and x_2 .

2.3. Models with asymmetric mutualism effects

We can also have a combination of the situations shown in the models (9) and (13), in which x_2 reduces the death rate of x_1 and x_1 increases the birth rate of x_2 , which allows for the modelling of interacting species with very different vital parameters, as follows:

$$\begin{aligned} x'_1 &= r_1 x_1 [a_1(x_1) - f_1(x_1, x_2)], \\ x'_2 &= r_2 x_2 [f_2(x_2, x_1) - a_2(x_2)]. \end{aligned} \tag{14}$$

Here, the assumptions on a_1 and f_1 are those used in the analysis of model (9) while for f_2 and a_2 we consider the assumptions from Equation (13). Again, the bounding theorems presented above hold with very similar proofs and the Dulac function is $\varphi(x_1, x_2) := 1/x_1 x_2 a_1(x_1) a_2(x_2)$, which leads to

$$\begin{aligned} & \frac{\partial}{\partial x_1} [\varphi(x_1, x_2) x'_1] + \frac{\partial}{\partial x_2} [\varphi(x_1, x_2) x'_2] \\ &= -\frac{r_1}{x_2 a_2(x_2)} \frac{\partial}{\partial x_1} \left[\frac{f_1(x_1, x_2)}{a_1(x_1)} \right] + \frac{r_2}{x_1 a_1(x_1)} \frac{\partial}{\partial x_2} \left[\frac{f_2(x_2, x_1)}{a_2(x_2)} \right] < 0. \end{aligned}$$

2.4. Mutualism model with strong Allee effects

We now assume that a strong Allee effect affects one of the species involved in a mutualistic interaction. Specifically, we shall replace the growth assumption (G) with the following *strong Allee effect assumptions*:

- (S1) $a(x) - f(x) < 0$ for $0 < x < A$,
- (S2) $a(x) - f(x) > 0$ for $A < x < K$,
- (S3) $a(x) - f(x) < 0$ for $x > K$,
- (S4) $a(A) - f(A) = a(K) - f(K) = 0$.

This ensures that a species with a strong Allee effect goes extinct if its density drops below the Allee threshold A and that A is now an unstable equilibrium of the model (8). If both species are subject to a strong Allee effect, then it is easy to see that the extinction state will always be a locally stable attractor. Hence, global stability of any coexistence equilibrium can only be addressed if just one of the species exhibits a strong Allee effect. In this case, the benefit this species gets from mutualism can be sufficiently strong to prevent its extinction when below A . We will establish a general condition for this to occur.

Let us consider the model (9) and assume that x_1 undergoes a strong Allee effect with the Allee threshold A_1 and the carrying capacity K_1 , while x_2 obeys the growth assumption (G) with the carrying capacity K_2 . In the absence of mutualism this system will have the following five equilibria $(0, 0)$, $(A_1, 0)$, $(K_1, 0)$, $(0, K_2)$, (A_1, K_2) , and (K_1, K_2) . Of these, $(0, K_2)$ and (K_1, K_2) are stable. In the presence of mutualism, assuming all other consistency conditions (C1), (C2) and (C3), if there exist a unique coexistence equilibrium of the model (9), then this equilibrium will be globally stable provided that all solutions are uniformly bounded in the positive quadrant. The boundedness arguments shown in the main two theorems of the previous section hold also here, with the caveat that we need to establish a condition which ensures that there is no limit point for any solution on a semi-axis.

While x_2 cannot go extinct due to the growth assumption (G), x_1 may approach zero because of the strong Allee effect assumptions (S1)–(S4). This may happen at the boundary equilibrium $(0, K_2)$. Evaluating the Jacobian of model (9) at this equilibrium we obtain

$$\begin{pmatrix} r_1[a_1(0) - f_1(0, K_2)] & 0 \\ -r_2K_2 \frac{\partial f_2}{\partial x_1}(K_2, 0) & r_2K_2 \left[a'_2(K_2) - \frac{\partial f_2}{\partial x_2}(K_2, 0) \right] \end{pmatrix}.$$

We see that the above matrix has two eigenvalues

$$r_1[a_1(0) - f_1(0, K_2)] \quad \text{and} \quad r_2K_2 \left[a'_2(K_2) - \frac{\partial f_2}{\partial x_2}(K_2, 0) \right].$$

The second eigenvalue is negative by the growth assumption (G). Hence, $(0, K_2)$ is unstable provided that

$$a_1(0) - f_1(0, K_2) > 0. \quad (15)$$

This represents the necessary and sufficient condition that species x_2 prevents the extinction of species x_1 and annihilates its strong Allee effect. If all other necessary conditions for the theorems in the previous section are met, then the coexistence equilibrium is globally stable.

3. Application to specific mutualism models

Here we apply our general results of the previous section to several specific, biologically motivated mutualism models, thus demonstrating broad utility of our approach.

3.1. Wolin–Lawlor model with weak Allee effect

Weak Allee effects are thought to be relatively common in nature, so it is natural to consider mutualism models with one or both species possessing a weak Allee effect. The following modification of model (2) allows for coverage of weak Allee effects

$$\begin{aligned} x'_1 &= r_1 x_1^{p_1} \left(1 - \frac{x_1}{K_1 + b_{12}x_2} \right), \\ x'_2 &= r_2 x_2^{p_2} \left(1 - \frac{x_2}{K_2 + b_{21}x_1} \right), \end{aligned} \quad p_1, p_2 \geq 1, \quad K_1, K_2 > 0. \quad (16)$$

In the absence of mutualism (i.e. for $b_{21} = b_{12} = 0$), Equation (16) decouple and each of them is of type (7). Therefore, if any of the exponents p_1, p_2 is greater than 1, then the respective species is subject to a weak Allee effect, while if both exponents are equal to 1, then there is no Allee effect and the model (16) reduces to the model (2).

It is easy to see that existence and uniqueness of a coexistence equilibrium E^* of model (16) is assured if and only if $b_{12}b_{21} < 1$. If this is the case, then

$$\begin{aligned} E^* &= (x_1^*, x_2^*), \quad x_1^* = \frac{K_1 + b_{12}K_2}{1 - b_{12}b_{21}}, \quad x_2^* = \frac{K_2 + b_{21}K_1}{1 - b_{12}b_{21}}, \\ a_1(x_1) &= x_1^{p_1-1}, \quad a_2(x_2) = x_2^{p_2-1}, \\ f_1(x_1, x_2) &= \frac{x_1^{p_1}}{K_1 + b_{12}x_2}, \quad f_2(x_2, x_1) = \frac{x_2^{p_2}}{K_2 + b_{21}x_1}, \end{aligned}$$

and consequently

$$\frac{a_1(x_1)}{f_1(x_1, \alpha x_1)} = \frac{K_1 + b_{12}\alpha x_1}{x_1}, \quad \frac{a_2(x_2)}{f_2(x_2, \alpha x_2)} = \frac{K_2 + b_{21}\alpha x_2}{x_2}.$$

This fits the framework of the general model (4) with $\mathcal{R}_1(\alpha) = b_{12}\alpha$, $\mathcal{R}_2(\alpha) = b_{21}\alpha$ and $\mathcal{R} = b_{12}b_{21}$. As a consequence, if $\mathcal{R} < 1$ then E^* is globally stable.

3.2. *q-Logistic Wolin–Lawlor model with weak Allee effect*

The classical logistic model of population growth with a linear per capita population growth rate is an idealization that is only rarely met in nature. Rather, relationships between the per capita population growth rate and population density are commonly non-linear, with convex relationships being more numerous [27]. A common model used to describe such non-linear relationships is $x' = rx(1 - (x/K)^q)$ for a positive parameter q [27]. We thus consider the following mutualism model with the generalized logistic term and possibly with a weak Allee effect

$$\begin{aligned} x_1' &= r_1 x_1^{p_1} \left(1 - \frac{x_1^{q_1}}{K_1^{q_1} + b_{12}x_2^{n_1}} \right), \\ x_2' &= r_2 x_2^{p_2} \left(1 - \frac{x_2^{q_2}}{K_2^{q_2} + b_{21}x_1^{n_2}} \right), \end{aligned} \tag{17}$$

assuming that $K_i > 0$, $p_i \geq 1$, $q_i > 0$ and $n_i > 0$ for $i = 1, 2$. For this model, we have

$$\begin{aligned} a_1(x_1) &= x_1^{p_1-1}, \quad a_2(x_2) = x_2^{p_2-1}, \\ f_1(x_1, x_2) &= \frac{x_1^{p_1+q_1-1}}{K_1^{q_1} + b_{12}x_2^{n_1}}, \quad f_2(x_2, x_1) = \frac{x_2^{p_2+q_2-1}}{K_2^{q_2} + b_{21}x_1^{n_2}}, \end{aligned}$$

and consequently

$$\frac{a_1(x_1)}{f_1(x_1, \alpha x_1)} = \frac{K_1^{q_1} + b_{12}\alpha^{n_1}x_1^{n_1}}{x_1^{q_1}}, \quad \frac{a_2(x_2)}{f_2(x_2, \alpha x_2)} = \frac{K_2^{q_2} + b_{21}\alpha^{n_2}x_2^{n_2}}{x_2^{q_2}}.$$

The consistency condition (C3) here requires that $n_1 \leq q_1$ and $n_2 \leq q_2$. If $n_1 < q_1$ then $\mathcal{R}_1(\alpha) = 0$ for all $\alpha > 0$, while if $n_1 = q_1$ we get $\mathcal{R}_1(\alpha) = b_{12}\alpha^{q_1}$. Similarly, if $n_2 < q_2$ then $\mathcal{R}_2(\alpha) = 0$ for all $\alpha > 0$, while if $n_2 = q_2$ then $\mathcal{R}_2(\alpha) = b_{21}\alpha^{q_2}$. It then follows that if $n_1 < q_1$ or $n_2 < q_2$ then the boundedness condition is satisfied for all other parameter values, while if $n_1 = q_1$ and $n_2 = q_2$ the boundedness condition is satisfied provided that

$$\mathcal{R} = (b_{12})^{1/q_1} (b_{21})^{1/q_2} < 1.$$

We provide an illustrative numerical example. Let $p_1 = p_2 = 1 + 10^{-4}$, $q_1 = n_1 = 3$, and $q_2 = n_2 = 1$. For $K_1 = 15$, $K_2 = 35$, $b_{12} = 0.75$, and $b_{21} = 0.7$ we see that $\mathcal{R} = 0.64$ and there is a unique equilibrium, which is globally stable. On the contrary, for $K_1 = 40$, $K_2 = 55$, $b_{12} = 2$, and $b_{21} = 1$ we have $\mathcal{R} = 1.38$ and the solutions are unbounded. In Figure 1 we show the phase portraits corresponding to these two situations, with $r_1 = 3 \times 10^{-5}$ and $r_2 = 1.05 \times 10^{-4}$ in panel (A) and $r_1 = 8 \times 10^{-5}$ and $r_2 = 1.65 \times 10^{-4}$ in panel (B). Note that the parameters r_1 and r_2 do not affect equilibrium stability but we set their values in order to plot the respective phase portraits.

In Figure 2 we show the region of a selected two-parameter space in which the solutions of the model (17) are bounded and we have a unique globally stable equilibrium. The shaded region corresponds to $\mathcal{R} < 1$. In panel (A), we compare the relative effect of the terms describing the mutualism effect, b_{12} and b_{21} . In panel (B), we compare the effect of a limiting resource term of one species (q_1) with the mutualistic effect of the other species (b_{12}). All other parameters are as considered for Figure 1.

We note that in the case $p_1 = p_2 = 1$ we obtain a q -logistic Wolin–Lawlor model with no Allee effect. If we further set $q_1 = q_2 = n_1 = n_2 = q > 0$, there is a unique positive equilibrium $\mathbf{E}^* = (x_1^*, x_2^*)$, with

$$x_1^* = \left(\frac{K_1^q + b_{12}K_2^q}{1 - b_{12}b_{21}} \right)^{1/q}, \quad x_2^* = \left(\frac{K_2^q + b_{21}K_1^q}{1 - b_{12}b_{21}} \right)^{1/q},$$

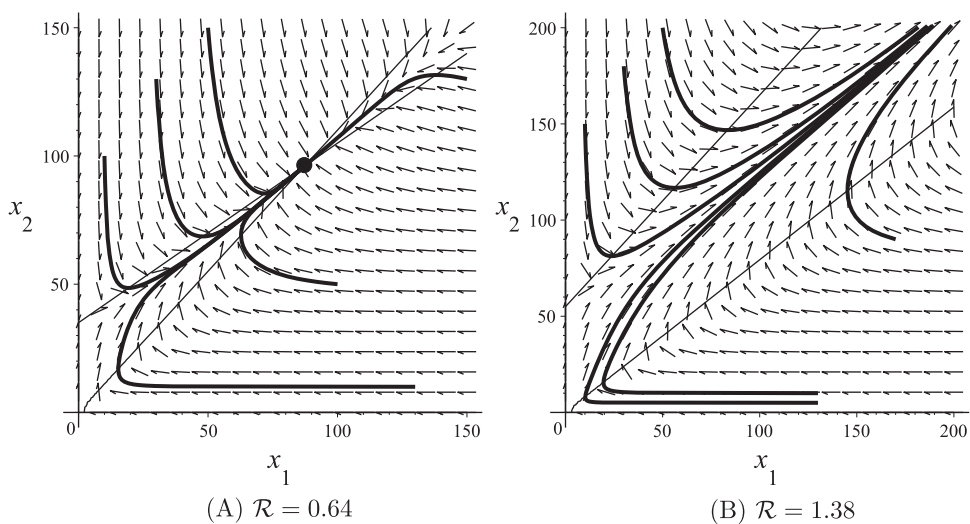


Figure 1. Phase portrait of model (17).

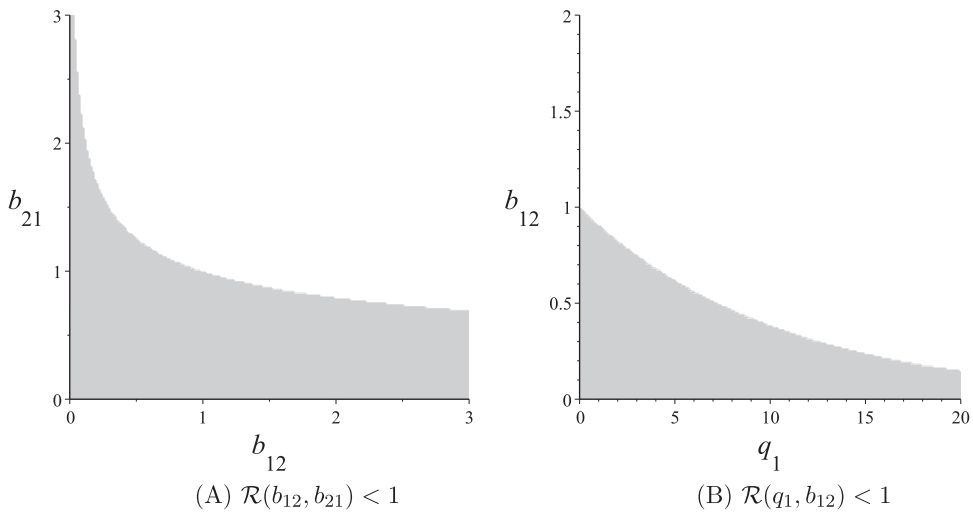


Figure 2. Global stability region for model (17).

if and only if $\mathcal{R} = b_{12}b_{21} < 1$, and this equilibrium is globally stable by Theorem 2.5. On the other hand, if $\mathcal{R} > 1$ the model solutions are unbounded by Remark 2.3.

3.3. Model with non-polynomial thresholds \mathcal{R}_1 and \mathcal{R}_2

For most published mutualism models, the limits \mathcal{R}_1 and \mathcal{R}_2 are powers of α . Nevertheless, our generalization does not require this particular form and for illustrative purposes we consider one example for which these limits have a different form, as follows:

$$\begin{aligned} x'_1 &= r_1 x_1 \left[1 - \frac{K_1 x_1}{1 + x_1} \left(1 + \frac{1}{1 + x_2} \right)^{x_1} \right], \\ x'_2 &= r_2 x_2 \left[1 - \frac{K_2 x_2}{1 + x_2} \left(1 + \frac{1}{1 + x_1} \right)^{x_2} \right], \end{aligned} \quad (18)$$

with $K_1 < 1$ and $K_2 < 1$. Then

$$\mathcal{R}_1(\alpha) = \frac{1}{K_1} e^{-1/\alpha}, \quad \mathcal{R}_2(\alpha) = \frac{1}{K_2} e^{-1/\alpha}.$$

The existence of a real number α such that $\mathcal{R}_1(\alpha) < 1$ and $\mathcal{R}_2(1/\alpha) < 1$ is now equivalent to

$$\mathcal{R} := \ln K_1 \ln K_2 < 1$$

and the solutions of model (18) are unbounded if the opposite inequality holds. For instance, if $K_1 = 0.3$ and $K_2 = 0.55$ then $\mathcal{R} = 0.72$, the solutions are bounded and we have a unique globally stable equilibrium (Figure 3(a)). On the other hand, if $K_1 = 0.23$ and $K_2 = 0.43$ and all the other parameters are the same then $\mathcal{R} = 1.24$ and all solutions are unbounded (Figure 3(b)). We have $r_1 = 0.002$ and $r_2 = 0.0033$ in panel (A) and $r_1 = 0.0026$ and $r_2 = 0.0042$ in panel (B).

In Figure 4 we plot the region of global stability when K_1 and K_2 vary.

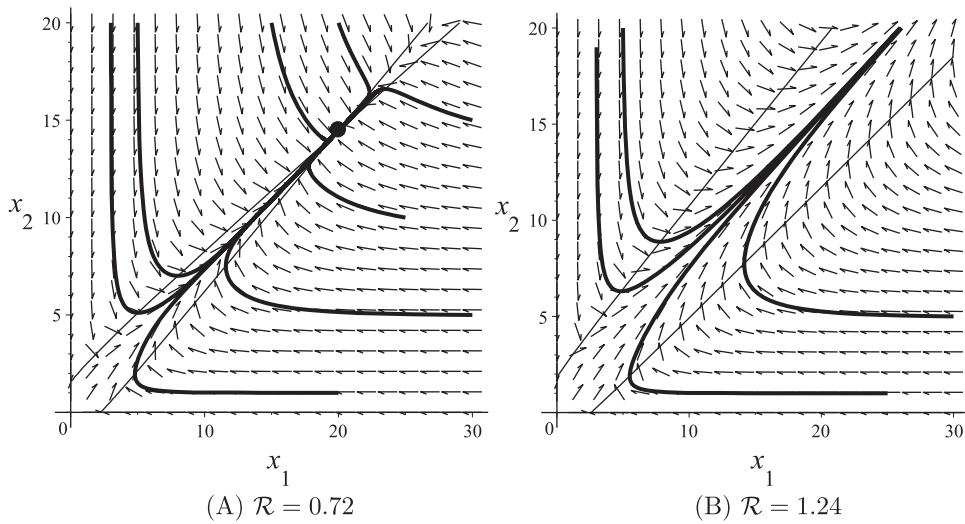


Figure 3. Phase portrait of model (18).

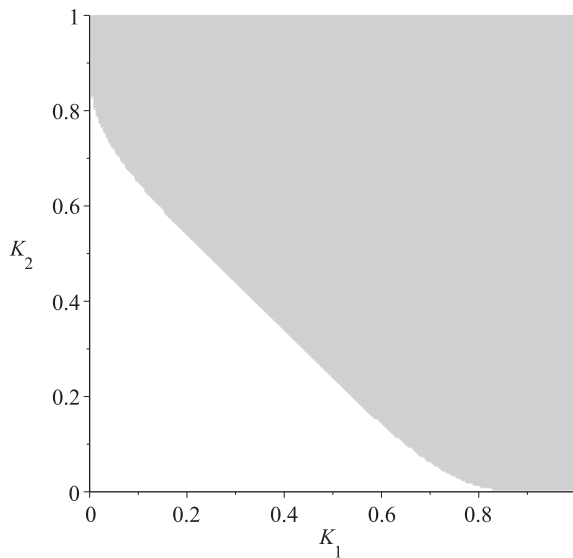


Figure 4. Global stability region for model (18), in which $\mathcal{R}(K_1, K_2) < 1$.

3.4. Model with mutualistic effects at low densities

In the previously considered mutualistic models (except Equation (18)), the mutualistic effect can be factored such that $f_i(x_1, x_2)$ is separated as a product of a function depending only on x_1 and a function depending only on x_2 . Our general results allow for models in which one cannot perform such a factorization. The following model exemplifies this situation

$$x_1' = r_1 x_1 \left(1 - \frac{x_1^{q_1}}{K_1^{q_1} + \frac{b_{12}}{1+x_1} x_2^{n_1}} \right),$$

$$x_2' = r_2 x_2 \left(1 - \frac{x_2^{q_2}}{K_2^{q_2} + \frac{b_{21}}{1+x_2} x_1^{n_2}} \right), \quad (19)$$

and has a biological appeal in describing the case when mutualism takes effect if the beneficiary species is at low densities and wanes as it grows. More specifically, the larger x_1 is the lower is its benefit gained from the presence of x_2 and vice versa. It is seen that

$$a_1(x_1) = 1, \quad a_2(x_2) = 1, \\ f_1(x_1, x_2) = \frac{x_1^{q_1}}{K_1^{q_1} + \frac{b_{12}}{1+x_1} x_2^{n_1}}, \quad f_2(x_2, x_1) = \frac{x_2^{q_2}}{K_2^{q_2} + \frac{b_{21}}{1+x_2} x_1^{n_2}},$$

and consequently

$$\frac{a_1(x_1)}{f_1(x_1, \alpha x_1)} = \frac{K_1^{q_1}}{x_1^{q_1}} + \frac{b_{12} \alpha^{n_1}}{x_1^{q_1-n_1} (1+x_1)}, \\ \frac{a_2(x_2)}{f_2(x_2, \alpha x_2)} = \frac{K_2^{q_2}}{x_2^{q_2}} + \frac{b_{21} \alpha^{n_2}}{x_2^{q_2-n_2} (1+x_2)}.$$

The consistency condition (C3) requires in this case that $q_1 \geq n_1$ and $q_2 \geq n_2$. However, $\mathcal{R}_1(\alpha) = \mathcal{R}_2(\alpha) = 0$ for all $\alpha > 0$, and the boundedness condition is thus satisfied. This is consistent with our previous interpretation: if mutualism wanes when the beneficiary species is at larger densities, there is less need to impose a further condition to prevent unboundedness.

Since the growth assumption (G) implies that $\mathcal{R}_1(0) < 1$ and $\mathcal{R}_2(0) < 1$, using the ideas of Theorems 2.2 and 2.6 and Remark 2.3 one may obtain the following result:

- Remark 3.1:** (1) If $\mathcal{R}_1(\alpha) < 1$ for all $\alpha > 0$ or $\mathcal{R}_2(\alpha) < 1$ for all $\alpha > 0$, then the solutions of model (9) are uniformly bounded.
- (2) If \mathcal{R}_1 and \mathcal{R}_2 are continuous and strictly increasing as functions of α and there are $a_1, a_2 \in (0, \infty)$ such that $\mathcal{R}_1(a_1) = \mathcal{R}_2(a_2) = 1$, then
- (a) if $a_1 a_2 > 1$, then the solutions of model (9) are uniformly bounded;
 - (b) if $a_1 a_2 < 1$, then the solutions of model (9) are unbounded.

3.5. Models with saturating functional response for mutualistic interaction

The Lotka–Volterra mutualism model (1) is a model of mutualism that fits the general formulation (3). Not surprisingly, our general theory gives for it the boundedness (and global stability) condition $b_{12} b_{21} < 1$, which is also the existence condition for its unique positive equilibrium. Here we consider another model that fits the general formulation (3). It is a modification of the Lotka–Volterra model that considers a saturating functional response for the mutualistic interaction. This model is commonly used in theoretical studies on mutualistic interactions and assumes that the effects of mutualists saturate as their density

becomes high [19, 31]. Here we consider a version proposed in [14] which has the form

$$\begin{aligned}x'_1 &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + c_1 x_1 (1 - e^{-\kappa_2 x_2}), \\x'_2 &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + c_2 x_2 (1 - e^{-\kappa_1 x_1}).\end{aligned}\tag{20}$$

For this model, the elements of Equation (3) are

$$\begin{aligned}f_1(x_1, x_2) &= 1 + \frac{c_1}{r_1} (1 - e^{-\kappa_2 x_2}), & a_1(x_1) &= \frac{x_1}{K_1}, \\f_2(x_2, x_1) &= 1 + \frac{c_2}{r_2} (1 - e^{-\kappa_1 x_1}), & a_2(x_2) &= \frac{x_2}{K_2},\end{aligned}$$

and consequently

$$\begin{aligned}\frac{f_1(x_1, \alpha x_1)}{a_1(x_1)} &= \frac{K_1}{x_1} \left[1 + \frac{c_1}{r_1} (1 - e^{-\kappa_2 \alpha x_1})\right], \\ \frac{f_2(x_2, \alpha x_2)}{a_2(x_2)} &= \frac{K_2}{x_2} \left[1 + \frac{c_2}{r_2} (1 - e^{-\kappa_1 \alpha x_2})\right].\end{aligned}$$

It then follows that

$$\mathcal{R}_1(\alpha) = \mathcal{R}_2(\alpha) = 0$$

implying that the solutions of model (20) are bounded. Since there is always a unique positive equilibrium of model (20) (see, for instance [13]), this equilibrium is globally stable. The same results hold also for a Holling type II formulation of the saturating functional response [19, 31].

3.6. Models with structurally different equations

To exemplify a biologically plausible case for which the mutual effects of mutualists may not be symmetric, we consider here a model that combines two structurally different equations

$$\begin{aligned}x'_1 &= r_1 x_1^p \left(1 - \frac{x_1}{K_1 + b_{12} x_2}\right), \\x'_2 &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + c_2 x_2 (1 - e^{-\kappa_1 x_1}),\end{aligned}\tag{21}$$

where h and c are some positive parameters. The first equation comes from the Wolin–Lawlor model with weak Allee effect (16) and may represent a plant that is able to grow also vegetatively but for which pollinators attracted when plant densities are higher significantly and increasingly contribute to the per capita population growth rate. The second equation comes from the model (20) and may represent a pollinator species the beneficial effect of which does not increase much more when its density is already high enough.

Using the notation from (14) we have that

$$\begin{aligned} a_1(x_1) &= x_1^{p-1}, \quad f_1(x_1, x_2) = \frac{x_1^p}{K_1 + b_{12}x_2}, \\ f_2(x_2, x_1) &= 1 + \frac{c_2}{r_2}(1 - e^{-\kappa_1 x_1}), \quad a_2(x_2) = \frac{x_2}{K_2}. \end{aligned}$$

Therefore,

$$\begin{aligned} \frac{a_1(x_1)}{f_1(x_1, \alpha x_1)} &= \frac{K_1 + b_{12}\alpha x_1}{x_1}, \\ \frac{f_2(x_2, \alpha x_2)}{a_2(x_2)} &= \frac{K_2}{x_2} \left[1 + \frac{c_2}{r_2}(1 - e^{-\kappa_1 \alpha x_2}) \right]. \end{aligned}$$

Then,

$$\mathcal{R}_1(\alpha) = b_{12}\alpha \quad \text{and} \quad \mathcal{R}_2(\alpha) = 0.$$

The coordinates of the positive equilibrium $E^* = (x_1^*, x_2^*)$ should satisfy the relations

$$\begin{aligned} K_1 + b_{12}x_2^* &= x_1^*, \\ r_2 \left(1 - \frac{x_2^*}{K_2} \right) + c_2(1 - e^{-\kappa_1 x_1^*}) &= 0, \end{aligned}$$

which leads to x_2^* being a solution of the equation

$$f(x_2) = 0, \tag{22}$$

with

$$f(x_2) = \frac{r_2 x_2}{K_2} + c_2 e^{-\kappa_1(K_1 + b_{12}x_2)} - (r_2 + c_2).$$

Since $f(0) < 0$, $\lim_{x_2 \rightarrow \infty} f(x_2) = +\infty$, f is continuous and

$$f''(x_2) = c_2(\kappa_1 b_{12})^2 e^{-\kappa_1(K_1 + b_{12}x_2)} > 0 \quad \text{for all } x_2 > 0,$$

it follows that Equation (22) has a single positive solution and, consequently, Equation (21) has a unique coexistence equilibrium, which is globally stable.

3.7. Models with strong Allee effect

Although strong Allee effects are quite difficult to detect in nature, some convincing examples exist and indirect evidence suggests there are even more of them [6]. As we emphasize in the previous section, a globally stable coexistence equilibrium is not possible if both species are subject to a strong Allee effect. But even when just one of the species is subject to a strong Allee effect, a beneficial effect of the other species need not always prevent that Allee effect. In other words, condition (15) need not be always satisfied, as we show in the following example.

Consider a species subject to a strong Allee effect that follows model (6) when alone. A possible mutualism model is then

$$\begin{aligned}x_1' &= r_1 x_1 \left[\left(\frac{1}{A_1} + \frac{1}{K_1} \right) x_1 - \frac{A_1 K_1 + x_1^2}{A_1 K_1 + b_{12} x_2} \right], \\x_2' &= r_2 x_2 \left(1 - \frac{x_2}{K_2 + b_{21} x_1} \right).\end{aligned}\tag{23}$$

In this setting

$$a_1(x_1) = \left(\frac{1}{A_1} + \frac{1}{K_1} \right) x_1, \quad f_1(x_1, x_2) = \frac{A_1 K_1 + x_1^2}{A_1 K_1 + b_{12} x_2},$$

and it is clear that condition (15) cannot hold. On the other hand, our boundedness theorem still applies. Since

$$R_1(\alpha) = \frac{(K_1 + A_1)b_{12}\alpha}{A_1 K_1}, \quad R_2(\alpha) = b_{21}\alpha,$$

it follows that model (23) has bounded solutions whenever

$$\mathcal{R} := \frac{b_{12}b_{21}(A_1 + K_1)}{A_1 K_1} < 1.$$

On the other hand, if $\mathcal{R} > 1$ then all solutions are unbounded except those starting in the basin of attraction of the boundary equilibrium $(0, K_2)$, which describes presence of a strong Allee effect in spite of the mutualism.

On the contrary, the following example describes a situation in which mutualism can overcome an existing strong Allee effect, condition (15) holds and there is a unique coexistence equilibrium that is globally stable. The mutualism model is as follows:

$$\begin{aligned}x_1' &= r_1 x_1 \left(A_1 e^{x_1} - \frac{B_1 + x_1 e^{x_1}}{1 + b_{12} x_2} \right), \\x_2' &= r_2 x_2 \left(1 - \frac{x_2}{K_2 + b_{21} x_1} \right).\end{aligned}\tag{24}$$

In this case

$$a_1(x_1) = A_1 e^{x_1}, \quad f_1(x_1, x_2) = \frac{B_1 + x_1 e^{x_1}}{1 + b_{12} x_2}.$$

The per capita growth rate of the first species in the absence of mutualism, $a_1(x_1) - f_1(x_1, 0)$, has a critical point at $x_1 = A_1 - 1$. Hence, in order to satisfy the strong Allee effect assumptions (S1)–(S4), we need to set the parameters A_1 and B_1 so that

$$e^{A_1-1} > B_1 > A_1 > 1.\tag{25}$$

This ensures that, in the absence of mutualism, the first species is subject to a strong Allee effects and has a hump-shaped per capita growth rate that equals zero at two different

positive values of x_1 . Since

$$R_1(\alpha) = A_1 b_{12} \alpha, \quad R_2(\alpha) = b_{21} \alpha,$$

model (24) has bounded solutions if and only if

$$\mathcal{R} := b_{12} b_{21} A_1 < 1.$$

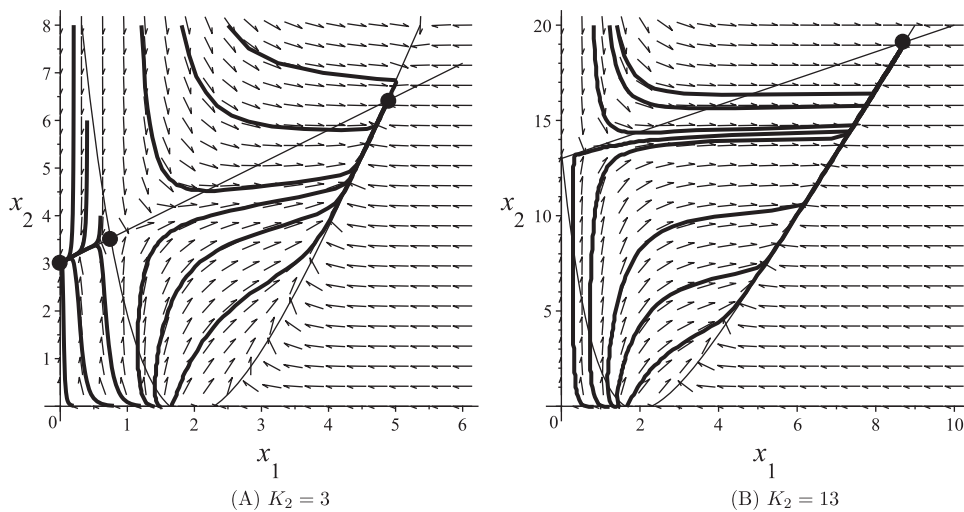


Figure 5. Phase portrait of model (24).

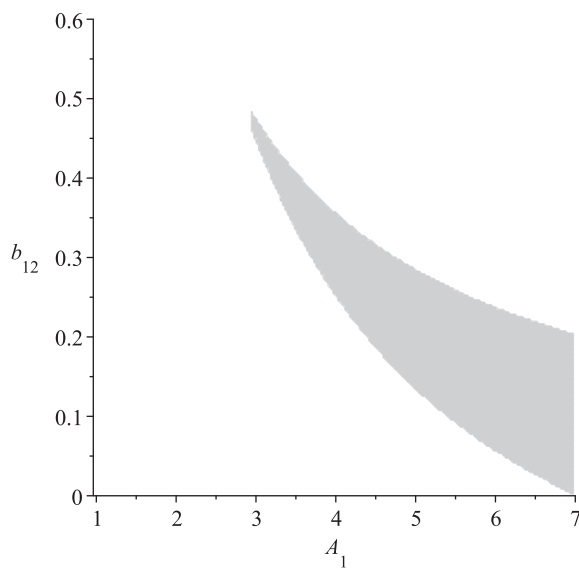


Figure 6. The region where mutualism eliminates the strong Allee effect in the model (24).

In addition, the strong Allee effect is eliminated in the first species if and only if condition (15) holds, which in this particular case requires that

$$A_1 > \frac{B_1}{1 + b_{12}K_2}. \quad (26)$$

We provide a numerical example to show that conditions (25) and (26) can indeed be satisfied simultaneously. Choosing $A_1 = 3$, $B_1 = 7$, $b_{12} = 0.1$, and $b_{21} = 0.7$ we have that $\mathcal{R} = 0.21$. If $K_2 = 3$, then the strong Allee effect in the first species is maintained and the boundary equilibrium $(0, K_2)$ remains locally stable (Figure 5(a)). On the other hand, if $K_2 = 13$ then $(0, K_2)$ becomes a saddle and the first species will never go extinct since mutualism prevents the strong Allee effect (Figure 5(b)). In Figure 6, we show the region given by the parameter that controls a vital rate of the first species (A_1) and the parameter describing the beneficial effect of the other species (b_{12}) in which the strong Allee effect in the first species is eliminated.

4. Conclusions

In this article, we extend the work of Georgescu et al. [12, 13] and provide a general class of models of facultative mutualism that covers many of the commonly used mutualism models. Most importantly, we study boundedness of solutions of models in this general class which, from the biological perspective, is an important necessary condition for any mutualism model to be considered plausible. The main theorems we provide in this respect allow for a much greater flexibility in designing these models. Formulations of the mutualistic interaction can now be more complex (i.e. do not require a factorization in the state variables) and each species can be modelled under different assumptions (e.g. one can benefit from a reduction in mortality and the other from an increase in fertility). Our generalization is therefore suitable for modelling mutualistic systems in which the interacting species are very different with respect to their vital parameters but also to their demographic assumptions. In addition, our generalization covers Allee effects as a part of mutualism models. This is certainly relevant, since at small population sizes or low population densities Allee effects (and especially weak Allee effects) are known to be relatively common (see, for instance, [5]). Mutualism models with Allee effects form just a specific case of our general model class, so they can be treated without any additional overhead provided that some general assumptions are met. Therefore, the most important biological implication of the results established herein is that many more systems than before are now known to be stable and that the presented models may become more adequate descriptions of mutualisms in models of more complex food webs.

Virtually all published mutualism models, including all we present in this article, follow a tradition set by Lotka and Volterra and have a logistic-like model or its Allee effect variant as their core element. Because of that, there is no clear distinction between birth and death rates in these models and both positive (or growth) and negative (or self-limiting) model terms comprise a piece of each. An alternative, more mechanistic approach would be to start with a model in which birth and death rates are explicit right from the beginning, such as

$$x' = x[b(x) - d(x)], \quad (27)$$

where the positive functions b and d represent the per capita birth and death rates, respectively. Mutualistic effects could then be classified as those that affect births, deaths, or both terms. Note that the single-species model (8) we start from has the same structure as the model (27). Therefore, if any mutualistic extension of the model (27) satisfies our assumptions, the general results we derive would apply also to this class of models. In addition, with birth and death rates clearly defined, the ratios \mathcal{R}_1 and \mathcal{R}_2 which enter all our general results would technically represent births to deaths ratios at given population densities and would thus be somewhat akin to reproductive ratios that characterize infection dynamics in epidemiology or population dynamics in life history theory. See also [10] for further discussion on related matters.

Some limitations of our work still exist, which may serve as potential avenues for further research. First of all, the consistency condition (C2) is far more restrictive than the similar condition (C1). This is due to our choice of the Dulac function used in our global stability argument. Presumably, a more elaborate Dulac function may allow a weaker condition in place of (C2). On the other hand, this may require more information about the structure of functions a_i and f_i and so there is likely to be a trade-off between how general these functions are and how less restrictive the Dulac function can be. In this paper, we place more importance on the solution boundedness results (required for biological plausibility) and on generality of mutualism models. While the derived conditions on bounded and unbounded solutions are mutually exclusive and in many cases threshold-like, the issue of uniqueness of a coexistence equilibrium is a separate question and does not follow directly from these conditions. It would certainly be of interest if a generalization were made so that uniqueness of a coexistence equilibrium follows from further suitable conditions on the right-hand sides of our generalized mutualism models. We expect to pursue these questions in a follow-up paper.

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