



Global stability of coexistence equilibria for n -species models of facultative mutualism

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ABSTRACT

We further pursue an investigation on an abstract model characterizing the dynamics of a general class of n -species facultative mutualisms that was initiated in Georgescu et al. (2017), establishing biologically relevant sufficient conditions for the global asymptotic stability of the coexistence equilibria. These conditions are given in terms of per-species limits of growth-to-loss ratios computed at higher population densities, complemented by either monotonicity or sublinearity inequalities, and are observed to hold for n -species versions of mutualistic models in current use. The specific modeling details that require either of these conditions being satisfied are outlined and discussed. As mutualisms can enhance species diversification and facilitate stable coexistence via a plethora of mechanisms, it is then important to understand the stability of speciose mutualisms, our results being of potential interest to theoretical ecologists studying the coexistence of many interacting species and to conservationists aiming for rare species preservation.

1. Introduction

A mutualism is an interaction between two or more species that is beneficial for all of them, fact often manifested in an increased ability to survive, grow or reproduce. There is a staggering diversity of mutualisms such as pollination (Richman et al., 2017), seed dispersal (Vander Wall et al., 2017), protection from antagonists or harsh environmental conditions (Trager et al., 2010), and the exchange of resources (Kang et al., 2011).

By the degree of dependency, mutualisms can be termed as obligate, when the mutualistic interactions are essential for species survival, and facultative, when either of the species can survive in the absence of others. For instance, a plant that is not able to produce seeds whenever a single pollinator species is absent engages in an obligate mutualism with its pollinator, while a plant that can either self-pollinate or can be pollinated by multiple species is involved in a facultative mutualism.

It is also argued that mutualisms are rarely one-to-one interactions, each species usually interacting with multiple mutualists that may also be expected to interact with each other (Richman et al., 2017). Understanding the dynamics of such multi-species interactions is then essential for an accurate assessment of coevolution as a means of reciprocal adaptive change. It has been noted in Cosmo et al. (2023) that coevolution can buffer against the adverse effects of environmental changes via facilitating colonization, thereby preventing species extinction and the collapse of metacommunities. In this regard, mutualisms

can increase the potential of dispersal, as well as allow species to expand their niches by increasing environmental suitability. Trait complementarity may then increase the overall survival and reproduction of mutualistic partners, but may also lead to highly specialized interactions in which the loss of a mutualistic partner increases the risk of coextinction.

Mutualisms are ubiquitous in nature, representing the very foundation of many ecosystems (corals and zooxanthellae, plants and mycorrhizal fungi, plants and pollinators, lichen-forming fungi and algae), as noted in Asplund and Wardle (2017). Some mutualisms (eukaryotes-mitochondria, plants-chloroplasts, angiosperms-pollinators, corals, lichens) were found to span thousands of species and hundreds of millions of years, the oldest mutualisms being significantly older than the oldest antagonisms across all organisms and within a wide range of taxa (Zeng and Wiens, 2021a). This provides strong evidence for the long-term stability of mutualisms, fact usually associated with mutualisms having higher overall diversification rates (Zeng and Wiens, 2021b).

In spite of their ubiquity, mutualisms have been somewhat neglected by theoretical ecologists and mathematicians alike. Part of the reason is probably historical, as the seminal works of Lotka and Volterra discussed models for competition and predation, but not for mutualism, although this does not entirely explain the subsequent orthodoxy of

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assuming that competition and predation are the most worthy forms of interaction for the development of a theoretical apparatus (Vandermeer and Goldberg, 2003). Also, even for a basic model of mutualism such as the one in Gause and Witt (1935) the solutions grow unbounded if the mutualistic inter-species support is strong enough also came in the way. This helped the onset of the idea that models of mutualism are shaky grounds, as they easily exhibit biologically unrealistic behavior. In his celebrated paper (May, 1976), May argued that Lotka–Volterra models are completely inadequate to represent mutualisms, as “they tend to lead to silly solutions in which both populations undergo unbounded exponential growth, in an orgy of mutual benefaction”. This underscores the idea that unboundedness of solutions is something that looms over many models of mutualism and one of the first steps in assessing the adequacy of such a model is proving the boundedness of all solutions.

In Georgescu et al. (2017), a framework for proving boundedness results for n -species models of mutualism in terms of threshold quantities that are computed at large population sizes has been assembled under fairly general assumptions and illustrated via treating several models of mutualism in common use. However, no attempt at establishing stability results has been made in Georgescu et al. (2017), although results in this direction have been obtained for the 2-dimensional case and for an earlier version of the framework in Maxin et al. (2017), further stability results for general 2-species models of mutualism being obtained in Vargas-De-León (2012) and Georgescu et al. (2016) via the use of Lyapunov functionals. Note that the approach employed in Maxin et al. (2017) makes explicit use of Dulac criterion and, as such, is not immediately extendable to a higher dimensional case. Also, we are not aware of generic stability results via Lyapunov’s second method for n -species mutualisms.

A comprehensive review of historical models of pairwise mutualism has been performed in Hale and Valdovinos (2021) with the purpose of finding stability patterns that are robust across assumptions, models and biosystems. It has been observed that mutualisms tend to exhibit stable coexistence at high population densities when benefits saturate and that mutualisms with at least one obligate partner exhibit destabilizing thresholds at low densities, diverse and well-characterized ecological mechanisms that amount to minimal realism in terms of limited benefits, accumulating costs, or accelerating intraspecific competition and permit stable coexistence being delineated. In fact, under alternative (biological, essentially amounting to resilience) definitions of stability involving persistence of populations or return time to equilibrium, mutualisms can be even more stable than predation and competition (Wolyn and Lawlor, 1984).

In what follows, we shall continue investigating the framework introduced in Georgescu et al. (2017) under augmented assumptions, making use of its mutualistic character (that leads to a cooperative dynamical system) in order to obtain stability results. We are then concerned with the n -species Kolmogorov model

$$x'_i = x_i[a_i(x_i) - f_i(x_1, x_2, \dots, x_n)], \quad 1 \leq i \leq n, \tag{1}$$

in which a_i and f_i , $i \in \{1, 2, \dots, n\}$, are presumed to be C^1 functions, the latter being also positive. Throughout this paper, the following assumptions will be presumed to hold true.

(L) For each $i \in \{1, 2, \dots, n\}$, there is $K_i > 0$ such that $a_i(K_i) - f_i(0, \dots, 0, K_i, 0, \dots, 0) = 0$ and

$$(x_i - K_i) (a_i(x_i) - f_i(0, \dots, 0, x_i, 0, \dots, 0)) < 0 \text{ for } x_i \neq K_i.$$

(M) For each $i \in \{1, 2, \dots, n\}$, $\frac{\partial f_i}{\partial x_j}(x) \leq 0$ for $x \in \mathbb{R}_+^n$ and $j \neq i$.

(NV) For each $i \in \{1, 2, \dots, n\}$, $\liminf_{\|x\| \rightarrow \infty} f_i(x) > 0$.

(C1) For each $i \in \{1, 2, \dots, n\}$, $\frac{\partial f_i}{\partial x_i}(x) \geq 0$ for $x \in \mathbb{R}_+^n$.

(C2) For each $i \in \{1, 2, \dots, n\}$ and any arbitrary real constants $s_1, s_2, \dots, s_n > 0$,

$$\frac{d}{dx} \left(\frac{a_i(s_i x)}{f_i(s_1 x, \dots, s_n x)} \right) < 0 \text{ for } x > M_i$$

where $M_i = M_i(s_1 x, \dots, s_n x)$, $M_i > 0$.

While the a_i ’s represent growth rates for species i , $1 \leq i \leq n$, the f_i ’s represent its removal rates and consequently the model (1) describes a situation in which the mutualistic support leads to a reduction of the removal rates (for instance, via establishing successful group defense behavior). It should be noted, though, that certain models in which the mutualistic support leads to an increase in the growth rates such as the n -species versions of Graves et al.’s model (Graves et al., 2006) and Wright’s model (Wright and simple, 1989) can be recasted in the form (1) too, as it shall be illustrated below. However, this should be regarded as a particular property of those models, as Gause–Witt mutualisms (for instance) cannot be recasted in a similar form. Further, for a given model, a_i and f_i are defined up to a function of x_i only.

The logistic assumption (L) states that any species is subject to self-limiting dynamics if all other species are absent and that the mutualistic interactions are of a facultative type, rather than obligate, as the extinction of any species is off the table. Consequently, the trivial equilibrium is unstable as a direct outcome of (L) and will be of no further concern. Assumption (C1) further clarifies the specifics of the self-limiting dynamics, stating that if everything else is kept constant, the removal rate of the species i , $1 \leq i \leq n$, is increasingly dependent on the density of that species. The mutualistic assumption (M) asserts the effects of mutualism, namely the fact that increasing the population size of species j has a positive effect on species i , $1 \leq i, j \leq n$, $i \neq j$. The non-vanishing removal assumption (NV) asserts the fact that no amount of mutualistic support can completely overcome natural removal tendencies.

As argued in Holland et al. (2002), net effects to mutualists are likely monotonically saturating or unimodal functions of the density of their partners. For instance, in pollination mutualisms the amount of flowers pollinated increases with pollinator abundance, but as the fraction of flowers pollinated approaches unity, the additional contribution of new pollinators decreases. In assumption (C2), which essentially asserts the “relative” saturation of the benefits extracted from the mutualistic interaction at higher population sizes, the constants s_i , $1 \leq i \leq n$, represent population sizes with respect to a common measuring unit x . This assumption makes sure that the quantities given below are well-defined and finite:

$$\mathbf{R}_i(s_1, s_2, \dots, s_n) := \lim_{x \rightarrow \infty} \frac{a_i(s_i x)}{f_i(s_1 x, s_2 x, \dots, s_n x)}.$$

Note that the constants $\mathbf{R}_i(s_1, s_2, \dots, s_n)$, defined as limits of growth-to-loss ratios at high population densities, can be thought as reproductive numbers. They play a role that is essentially similar to that of a basic reproduction number in Mathematical Epidemiology (whose definition also uses the growth times removal to the power of -1 paradigm). Unlike the latter, they have a non-local nature, since they do not characterize the behavior of (1) in the vicinity of any point in particular, of concern being a problem of a very distinct nature (unbounded species growth, rather than disease eradication).

Let us state an additional assumption, meant to ensure the boundedness of the solutions of (1).

(B) The boundedness assumption There are $\alpha_i > 0$, $1 \leq i \leq n$, for which

$$\mathbf{R}_i(\alpha_1, \alpha_2, \dots, \alpha_n) < 1, \quad \text{for each } i \in \{1, 2, \dots, n\}.$$

Reviewing Theorems 2.1, 2.2 and Corollary 2.1 of Georgescu et al. (2017) (paper which, in fact, has a wider scope than proving boundedness), one obtains the following result that asserts the ecological well-posedness of (1).

Theorem 1.1. *If (B) holds, then there is at least a coexistence equilibrium of (1). Also, all solutions of (1) starting in $\text{int}(\mathbb{R}_+^n)$ ultimately enter a compact region A of $\text{int}(\mathbb{R}_+^n)$.*

The meaning of [Theorem 1.1](#) is that if losses exceed gains at high population densities, as quantified in assumption (B), then all populations sizes remain bounded for all future time. Note that [Theorem 1.1](#) is, in a sense, nontrivial, since it ensures the boundedness of *all* solutions via imposing conditions for *certain* relative population sizes. Further, this result is formulated in terms of n parameters (conditions), rather than in terms of a single one, as it is the case for the usual results concerning the stability of the equilibria in Mathematical Epidemiology (for obvious reasons, we think of boundedness as a precursor to the stability of positive equilibria). It is then natural to think about situations in which the boundedness conditions can be formulated in terms of a single parameter.

In what follows, we shall augment condition (B) with either sublinearity or monotonicity conditions and use a monotone dynamical systems approach to establish stability results for the coexistence equilibria of our model (1). To this purpose, the boundedness of solutions is seen in [Section 2](#) to be of paramount importance, as it drastically limits down a certain trichotomy perspective provided by the monotone dynamical systems approach. Next, we use in [Section 3](#) these stability results to discuss several higher-dimensional mutualistic models whose 2-dimensional versions are in current use, outlining the specific details that require a certain form of the stability results. Finally, [Section 4](#) is dedicated to further comments regarding the applicability of our results.

It has been argued in [Gómez and Verdú \(2012\)](#) via an analysis of phylogenetic, neontologic and paleontological information that mutualisms with plants fueled primate diversification by hampering extinction and increasing geographical speciation. More generally, [Chomicki et al. \(2019\)](#) listed and commented upon a plethora of mechanisms by which mutualisms are able to modulate species richness, viewed as a metric of diversification. It was noted that mutualisms can enhance diversification directly, via partner shifts or host-symbiont genetic incompatibility, or indirectly, via increasing ecological opportunities, or via decreasing extinction by enlarging range size or enhancing individual survival. If mutualisms influence diversification, it is then important to understand the stability of speciose mutualisms, which is the eventual goal of this paper. Conversely, mutualisms can decrease lineage diversification by means of “stabilizing coevolution” processes, via increased trait matching, restriction by hosts of the genetic diversity of the symbiont and via increasing the risk of extinction by decreasing the realized niche of a species, reducing niche breadth, or associating partner loss with a high fitness cost.

Further, as discussed in [Chomicki et al. \(2019\)](#), mutualisms can promote stable coexistence via altering the outcomes of competition, either by increasing negative intraspecific interactions (promoting asymmetry in the delivery of benefits), or by decreasing negative interspecific interactions (increasing niche differentiation and partitioning, promoting competition-colonization trade-offs among partners). They can also promote stable coexistence via equalizing effects that lead partnering species to be more equal in their competitive abilities, notably by locally altering competitive hierarchies across a variety of environmental conditions. As a result, a partner that is unsuitable under a certain set of conditions may become ideal under a different set, leading to species coexistence and ecosystem resilience as the environmental conditions change through space and time ([Chamberlain et al., 2014](#)).

Conversely (although this is a comparatively rarer outcome), mutualisms could restrict species coexistence by limiting dispersal and increasing relatedness in clustered populations of mutualists ([Akçay, 2017](#)), and by creating positive feedback that promotes the dominant species, thereby negatively impacting species coexistence ([Báez et al., 2016](#)). It then becomes of paramount importance to delineate and analyze the potential mechanisms of mutualism-facilitated stabilization

and coexistence within a given ecosystem, our results being then of potential interest to theoretical ecologists studying the coexistence of many interacting species and to conservationists aiming for rare species preservation.

2. Main results

For the sake of completeness, let us introduce a few notions and notations. For $x, y \in \mathbb{R}^n$, we shall write $x \leq y$ if $y - x \in \mathbb{R}_+^n$, $x < y$ if $y - x \in \mathbb{R}_+^n \setminus \{0\}$ and $x \ll y$ if $y - x \in \text{int}(\mathbb{R}_+^n)$.

We shall denote by $\sigma(A)$ the spectrum (eigenset) of a given square matrix A and by $s(A)$ its spectral abscissa, defined as the maximal real part of an eigenvalue. Accordingly, a square matrix A will be called Hurwitz stable if $s(A) < 0$. Further, a square matrix A will be called a Metzler matrix if all its off-diagonal components are non-negative.

Given a $n \times n$ matrix A , one defines a directed graph $G(A)$ with $1, 2, \dots, n$ as its vertices in such a way that there is an arc from j to k , $1 \leq j, k \leq n$, iff $a_{jk} \neq 0$. A is then called irreducible if any two distinct vertices of $G(A)$ can be joined by an oriented path.

For $f : \mathbb{R}_+^n \rightarrow \mathbb{R}^n$, one denotes by $Df(x)$ the Jacobian matrix of f computed at x . If $Df(x)$ is a Metzler matrix for all $x \in \mathbb{R}_+^n$, f is then called cooperative. We shall also say that h is sublinear on \mathbb{R}_+^n if $h(\alpha x) > \alpha h(x)$ for any $\alpha \in (0, 1)$ and $x \gg 0$. Obviously, if h is concave and $h(0) = 0$, then h is also sublinear.

2.1. Conditions leading to boundedness

Unfortunately, although conceptually meaningful, condition (B) is difficult to verify in concrete situations, as it requires finding not a single one but n parameters satisfying not-so-transparent conditions. We shall now comment upon its reformulation in a certain specific situation. To this goal, let us assume that the reproductive numbers have the quasi-polynomial expression

$$\mathbf{R}_i(s_1, s_2, \dots, s_n) = \sum_{k=1, k \neq i}^n C_{ik} \left(\frac{s_k}{s_i} \right)^p, \quad i \in \{1, 2, \dots, n\}, \quad (2)$$

motivated by a certain specific model ([Wolin and Lawlor, 1984](#)) that will be indicated in [Section 3](#), with

$$C_{ik} \geq 0 \quad \text{for all } 1 \leq i \neq k \leq n.$$

As done in [Georgescu et al. \(2017\)](#), define the Metzler matrix C by

$$C = \begin{pmatrix} -1 & C_{12} & \dots & C_{1n} \\ C_{21} & -1 & \dots & C_{2n} \\ \vdots & \vdots & \dots & \vdots \\ C_{n1} & C_{n2} & \dots & -1 \end{pmatrix}. \quad (3)$$

and observe ([Georgescu et al., 2017](#), [Theorem 3.1](#)) that condition (B) is equivalent to condition (H) below.

(H) The matrix C is Hurwitz stable.

Note that the boundedness of (1) is now expressed in terms of a matrix-related single parameter, the spectral abscissa of C , which brings the situation more in line with the definition and usage of a (single) basic reproduction number in Mathematical Epidemiology. Since the matrix C is a Metzler matrix whose main diagonal elements are negative, this is further equivalent to the following more palatable practical stability condition ([Poole and Bouillion \(1974\)](#), [Theorem 2.1](#)).

(S) The i th leading minor of C has sign $(-1)^i$, $i \in \{1, 2, \dots, n\}$.

Further, we observe ([Georgescu et al., 2017](#), [Theorem 3.1](#)) that condition (U) below implies the existence of unbounded solutions.

(U) The matrix C is Hurwitz unstable and irreducible.

2.2. Stability under sublinearity conditions

Let us now turn our attention back to system (1). No claim towards the uniqueness of the coexistence equilibrium or its stability have been made in Georgescu et al. (2017), as those specific objectives are not within the reach of the approach employed therein. However, having in view that (1) is cooperative in the sense of the definition given above, boundedness is a decisive first step towards stability, as seen from the following trichotomy result, established in Zhao and Jing (1996).

Theorem 2.1 (Zhao and Jing, 1996). *Given the system $x' = h(x)$, $h : \mathbb{R}_+^n \rightarrow \mathbb{R}^n$ being a C^1 map, assume that*

1. h is cooperative and $Dh(x)$ is irreducible for all $x \in \mathbb{R}_+^n$;
2. $h(0) = 0$ and $h_i(x) \geq 0$ for any $x \in \mathbb{R}_+^n$ such that $x_i = 0$, $i \in \{1, 2, \dots, n\}$;
3. h is strictly sublinear.

Then the following statements hold.

1. If $s(Dh(0)) \leq 0$, then $x = 0$ is globally asymptotically stable in \mathbb{R}_+^n .
2. If $s(Dh(0)) > 0$ and $\psi(t, y_0)$ is the saturated solution of $x' = h(x)$ starting in y_0 , then either
 - (a) For all $y_0 \in \mathbb{R}_+^n \setminus \{0\}$, $\lim_{t \rightarrow \infty} |\psi(t, y_0)| = +\infty$, or
 - (b) The system $x' = h(x)$ admits a unique coexistence equilibrium x^* which is globally asymptotically stable in $\mathbb{R}_+^n \setminus \{0\}$.

Under the hypotheses of Theorem 2.1, once $s(Dh(0)) > 0$ and the boundedness of the trajectories is ensured, then the global asymptotic stability of the coexistence equilibrium follows. Also, the existence of a coexistence equilibrium or the availability of a persistence result preclude the global asymptotic stability of the origin.

If the sublinearity assumption is dropped and the positivity of the spectral abscissa $s(Dh(0))$ is a priori assumed, then the following dichotomic attractivity result holds.

Theorem 2.2 (Zhao and Jing, 1996). *Given the system $x' = h(x)$, with $h : \mathbb{R}_+^n \rightarrow \mathbb{R}^n$ being a C^1 map, assume that*

1. h is cooperative and $Dh(x)$ is irreducible for all $x \in \mathbb{R}_+^n$;
2. $h(0) = 0$ and $h_i(x) \geq 0$ for all $x \in \mathbb{R}_+^n$ such that $x_i = 0$, $i \in \{1, 2, \dots, n\}$;
3. $s(Dh(0)) > 0$.

Then either

1. For all $y_0 \in \mathbb{R}_+^n \setminus \{0\}$, $\lim_{t \rightarrow \infty} |\psi(t, y_0)| = +\infty$, or
2. There is a coexistence equilibrium x^* of the system $x' = h(x)$ such that for each y_0 satisfying $0 < y_0 \leq x^*$, $\lim_{t \rightarrow \infty} \psi(t, y_0) = x^*$. Moreover, for any $y_0 > 0$, $\liminf_{t \rightarrow \infty} \psi(t, y_0) \geq x^*$.

For the system (1) of concern, denoting by h its right-hand side, we note that $h(0) = 0$, h is cooperative due to (M) and

$$Dh(x) = D(x) - J(x), \tag{4}$$

with

$$D(x) = \text{diag}(a_i(x_i) + x_i a'_i(x_i) - f_i(x)), \quad 1 \leq i \leq n \tag{5}$$

$$J(x) = (J_{ij}(x))_{1 \leq i, j \leq n}, \quad J_{ij}(x) = x_i \frac{\partial f_i}{\partial x_j}(x). \tag{6}$$

Also, the sublinearity condition reduces to

$$a(\alpha x) - f(\alpha x) > \alpha(x) - f(x), \quad \text{for any } \alpha \in (0, 1) \text{ and } x \gg 0, \tag{SL}$$

where a and f are defined by $a(x) = (a_i(x_i))_{1 \leq i \leq n}$ and $f(x) = (f_i(x))_{1 \leq i \leq n}$, respectively. It is then seen that the following results hold.

Theorem 2.3. *Assume that $D(x) - J(x)$ is irreducible for all $x \in \text{int}(\mathbb{R}_+^n)$ and $s(D(0)) > 0$. Then either each solution of (1) that starts in $\mathbb{R}_+^n \setminus \{0\}$ is unbounded or there is a coexistence equilibrium x^* of (1) such that for any x with $0 \ll x \leq x^*$, $\lim_{t \rightarrow \infty} \psi(t, x) = x^*$. Moreover, in the latter case, for any $x \gg 0$, $\liminf_{t \rightarrow \infty} \psi(t, x) \geq x^*$. Further, if (SL) holds, then x^* is unique and globally asymptotically stable in $\text{int}(\mathbb{R}_+^n)$.*

Note that the persistence of the system (an outcome of (L)) is important since, as seen below, $D(x) - J(x)$ may not necessarily be irreducible on the boundary of \mathbb{R}_+^n . From a biological viewpoint, $s(D(0)) > 0$ characterizes the fact that (1) is indeed a facultative mutualism.

One then obtains the following practical stability criterion which is to be used when the reproductive numbers have the quasi-polynomial form (2).

Theorem 2.4. *Assume that the R_i 's are given by (2), $D(x) - J(x)$ is irreducible for all $x \in \text{int}(\mathbb{R}_+^n)$ and $s(D(0)) > 0$.*

1. If C is Hurwitz stable, then there is a coexistence equilibrium x^* of (1) such that for any x with $0 \ll x \leq x^*$, $\lim_{t \rightarrow \infty} \psi(t, x) = x^*$. Moreover, for any $x \gg 0$, $\liminf_{t \rightarrow \infty} \psi(t, x) \geq x^*$. Further, if (SL) holds, then x^* is unique and globally asymptotically stable in $\text{int}(\mathbb{R}_+^n)$.
2. If C is Hurwitz unstable and irreducible, then each solution of (1) that starts in $\mathbb{R}_+^n \setminus \{0\}$ grows unbounded.

2.3. Stability under monotonicity conditions

It will be seen in Section 3 that the sublinearity condition is not always satisfied in concrete situations. To deal with this shortcoming, let us note that the following related result which replaces sublinearity and irreducibility with a monotonicity condition for the associated Jacobian has been established in Smith (1986).

Theorem 2.5. *Given the system*

$$x'_i = x_i g_i(x_1, x_2, \dots, x_n), \quad 1 \leq i \leq n, \tag{7}$$

assume the following hypotheses

- (H1) G is cooperative;
- (H2) $G(0) \gg 0$;
- (H3) $DG(y) \geq DG(z)$ when $z \geq y \geq 0$,

G being the vector-valued function defined by $G(x) = (g_i(x))_{1 \leq i \leq n}$. If (7) has an equilibrium point in $\text{int}(\mathbb{R}_+^n)$, then this equilibrium point is unique in $\text{int}(\mathbb{R}_+^n)$ and also globally asymptotically stable in $\text{int}(\mathbb{R}_+^n)$.

Note that hypotheses (H1)–(H3) do not imply by themselves that there is a coexistence equilibrium by themselves; this should be established separately. Condition (H2), dealing in an ecological setting with the per capita growth rates in near-extinction conditions, ensures that (7) describes a facultative mutualism too. With a view to characterize the dynamics of (1), let us define

$$D_0(x) = \text{diag}(a'_i(x_i) + x_i a''_i(x_i) - f_i(x)) \quad 1 \leq i \leq n.$$

From Theorem 2.5, one obtains that the following result holds true.

Theorem 2.6. *If (B) holds and*

- (H2p) $a(0) - f(0) \gg 0$;
- (H3p) $D_0(y) - Df(y) \geq D_0(z) - Df(z)$ when $z \geq y \geq 0$,

then (1) has a unique coexistence equilibrium which is globally asymptotically stable in $\text{int}(\mathbb{R}_+^n)$.

As it will be seen below, Theorems 2.3 and 2.6 have distinct areas of applicability, even when the former is particularized to Kolmogorov systems (note that Theorem 2.3 can be applied to systems which are not in Kolmogorov form too). This, in turn, has the following practical stability consequence.

Theorem 2.7. Assume that the R_i 's are given by (2) and (S) holds, together with (H2p) and (H3p). Then (1) has a unique coexistence equilibrium which is globally asymptotically stable in $\text{int}(\mathbb{R}_+^n)$.

3. Applications

In what follows, we shall illustrate the applicability of our framework by discussing the stability of the coexistence equilibria for n -species versions of several widely used models of mutualism.

3.1. Wolin and Lawlor's model

Let us consider the n -species mutualistic model

$$x'_i = r_i x_i \left[A_i - \frac{x_i^p}{K_i + \sum_{k \neq i} b_{ik} x_k^p} \right], \quad 1 \leq i \leq n, \quad p \geq 1, \tag{8}$$

introduced in Georgescu et al. (2017) to enhance the model proposed in Wolin and Lawlor (1984) and May (1976), to which it reduces when $n = 2$ and $p = 1$. The model of Wolin and Lawlor (1984) assumes that the mutualism increases the carrying capacity of the environment with respect to the recipient species (in other words, benefits from mutualism reduce negative density dependence) and that the effects of mutualism are the most prominent at high recipient density. It is seen that

$$a_i(x_i) = r_i A_i, \quad f_i(x_1, x_2, \dots, x_n) = \frac{r_i x_i^p}{K_i + \sum_{k \neq i} b_{ik} x_k^p}$$

which implies that

$$\frac{a_i(s_i x)}{f_i(s_1 x, s_2 x, \dots, s_n x)} = A_i \left[\frac{K_i}{(s_i x)^p} + \sum_{k \neq i} b_{ik} \left(\frac{s_k}{s_i} \right)^p \right];$$

note that this decreases as a function of x . Consequently,

$$\begin{aligned} R_i(s_1, s_2, \dots, s_n) &= \lim_{s \rightarrow \infty} A_i \left[\frac{K_i}{(s_i x)^p} + \sum_{k \neq i} b_{ik} \left(\frac{s_k}{s_i} \right)^p \right] \\ &= A_i \left[\sum_{k \neq i} b_{ik} \left(\frac{s_k}{s_i} \right)^p \right], \end{aligned}$$

the associated matrix C having the form

$$C = \begin{pmatrix} -1 & A_1 b_{12} & \dots & A_1 b_{1n} \\ A_2 b_{21} & -1 & \dots & A_2 b_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ A_n b_{n1} & A_n b_{n2} & \dots & -1 \end{pmatrix}.$$

Also,

$$\begin{aligned} a_i(\alpha x) - f_i(\alpha x) &> a_i(x) - f_i(x) \\ \Leftrightarrow \frac{(\alpha x_i)^p}{K_i + \sum_{k \neq i} b_{ik} (\alpha x_k)^p} &< \frac{x_i^p}{K_i + \sum_{k \neq i} b_{ik} x_k^p} \\ \Leftrightarrow K_i + \sum_{k \neq i} b_{ik} (\alpha x_k)^p &> K_i \alpha^p + \sum_{k \neq i} b_{ik} (\alpha x_k)^p. \end{aligned}$$

which holds true for all $\alpha \in (0, 1)$ and $x \gg 0$. It is also seen that $D(x) - J(x)$ is given by

$$(D(x) - J(x))_{i,j} = \begin{cases} r_i \left[A_i - \frac{(p+1)x_i^p}{K_i + \sum_{k \neq i} b_{ik} x_k^p} \right], & i = j \\ \frac{r_i p b_{ij} x_i^{p+1} x_j^{p-1}}{(K_i + \sum_{k \neq i} b_{ik} x_k^p)^2}, & i \neq j, \end{cases}$$

which implies that $D(x) - J(x)$ is irreducible for any $x \in \text{int}(\mathbb{R}_+^n)$, since all off-diagonal elements are nonzero. Note that $D(x) - J(x)$ may be reducible on the boundary of \mathbb{R}_+^n (for instance, $D(x_*) - J(x_*)$ is reducible, with $x_* = (\sqrt[p]{\frac{K_1 A_1}{p+1}}, 0, \dots, 0)$. Further, $D(0) - J(0) = \text{diag}(r_i A_i), 1 \leq i \leq n$. It then follows that $s(D(0) - J(0)) = \max_{1 \leq i \leq n} r_i A_i > 0$. Consequently, the following stability result holds.

Theorem 3.1. There is a unique coexistence equilibrium of (8) which is globally asymptotically stable in $\text{int}(\mathbb{R}_+^n)$ provided that

$$\begin{aligned} \begin{vmatrix} -1 & A_1 b_{12} \\ A_2 b_{21} & -1 \end{vmatrix} > 0, \quad \begin{vmatrix} -1 & A_1 b_{12} & A_1 b_{13} \\ A_2 b_{21} & -1 & A_2 b_{23} \\ A_3 b_{31} & A_3 b_{32} & -1 \end{vmatrix} < 0, \dots, \\ (-1)^n \begin{vmatrix} -1 & A_1 b_{12} & \dots & A_1 b_{1n} \\ A_2 b_{21} & -1 & \dots & A_2 b_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ A_n b_{n1} & A_n b_{n2} & \dots & -1 \end{vmatrix} > 0. \end{aligned}$$

Note that for $n = 2$ the stability condition is $A_1 A_2 b_{12} b_{21} < 1$, in which case we obtain (Vargas-De-León, 2012, Proposition 1). Also, for $n = 3$, the stability conditions become

$$\begin{aligned} A_1 A_2 b_{12} b_{21} < 1, \quad A_1 A_2 b_{12} b_{21} + A_1 A_3 b_{13} b_{31} + A_2 A_3 b_{23} b_{32} \\ + A_1 A_2 A_3 (b_{12} b_{23} b_{31} + b_{13} b_{32} b_{21}) < 1, \end{aligned}$$

the second condition implying the first one.

Let us now note that while the hypotheses of Theorem 2.3 are satisfied, those of Theorem 2.6 are not.

Remark 3.1. Note that not all hypotheses of Theorem 2.6 are satisfied, since in this case

$$(D_0(x) - Df(x))_{i,j} = \begin{cases} -\frac{r_i p x_i^{p-1}}{K_i + \sum_{k \neq i} b_{ik} x_k^p}, & i = j \\ \frac{r_i p b_{ij} x_i^p x_j^{p-1}}{(K_i + \sum_{k \neq i} b_{ik} x_k^p)^2}, & i \neq j. \end{cases}$$

Consequently, condition (H3p) will not hold.

To illustrate Theorem 3.1, we have represented in Fig. 1 the regions of the A_1 - A_2 parameter space that lead to a globally stable coexistence equilibrium for a 3-dimensional version of (8). For Fig. 1, $\alpha_{12} = 0.1$, $\alpha_{21} = 0.3$, $\alpha_{13} = 0.4$, $\alpha_{31} = 0.2$, $\alpha_{23} = 0.6$, $\alpha_{32} = 0.2$, while $A_3 = 0.2$ (for (a)), $A_3 = 0.6$ (for (b)), $A_3 = 1.5$ (for (c)). Note that our parameter values are chosen for convenience and do not immediately correspond to any concrete mutualistic interaction, much like the values chosen for the other figures.

3.2. Wolin and Lawlor's model with a hyperconnected species

Let us now consider a particularization of (8) (also of concern in Georgescu et al. (2017)) which describes the situation in which the n th species is "hyper-connected", in the sense that it interacts with species 1, 2, ..., $n - 1$ that do not interact between themselves (see also Vargas-De-León (2015)). This may occur when the n th species is an exclusive pollinator for the other (plant) species 1, 2, ..., $n - 1$. In this case, (8) reduces to

$$\begin{cases} x'_1 = r_1 x_1 \left(A_1 - \frac{x_1^p}{K_1 + b_{1n} x_n^p} \right), \\ x'_2 = r_2 x_2 \left(A_2 - \frac{x_2^p}{K_2 + b_{2n} x_n^p} \right), \\ \vdots \\ x'_n = r_n x_n \left(A_n - \frac{x_n^p}{K_n + b_{n1} x_1^p + \dots + b_{n,n-1} x_{n-1}^p} \right) \end{cases} \tag{9}$$

and consequently

$$C = \begin{pmatrix} -1 & 0 & \dots & 0 & A_1 b_{1n} \\ 0 & -1 & \dots & 0 & A_2 b_{2n} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & -1 & A_{n-1} b_{n-1n} \\ A_n b_{n1} & A_n b_{n2} & \dots & A_n b_{n,n-1} & -1 \end{pmatrix}.$$

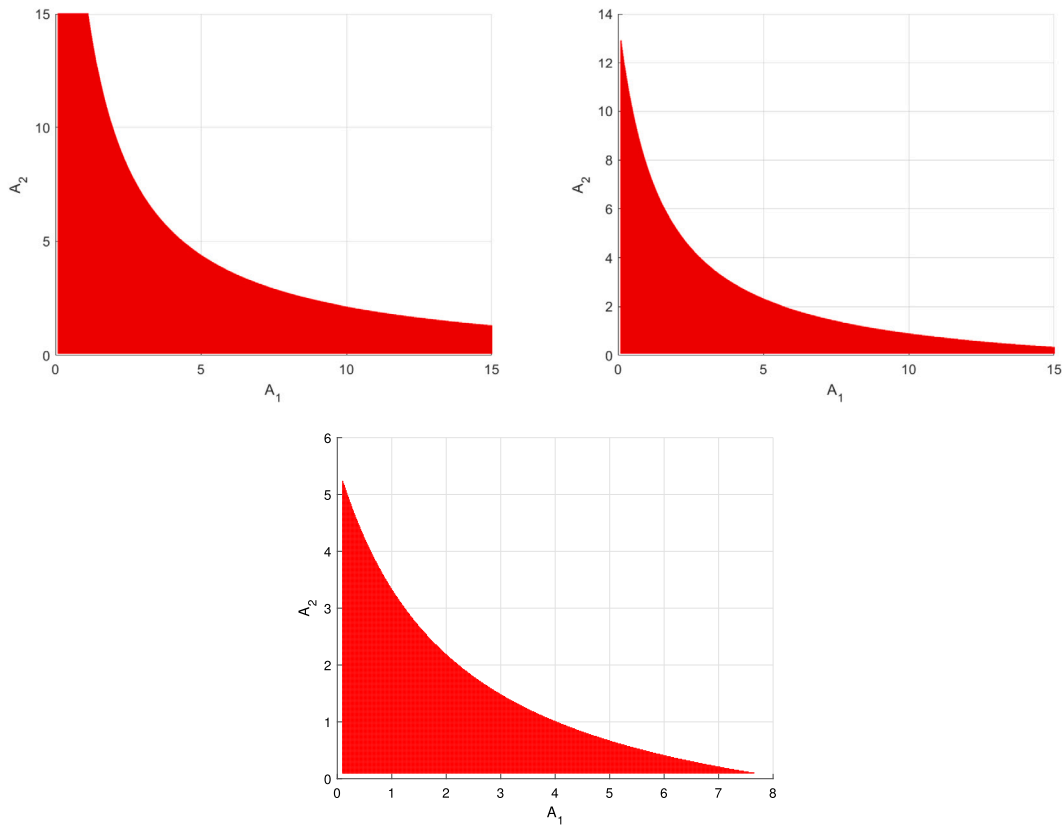


Fig. 1. Regions in the A_1 - A_2 plane leading to a globally stable coexistence equilibrium for a 3-dimensional version of (8) and distinct values of A_3 .

Observe that the p th order leading minors are equal to $(-1)^p$ for $p \in \{1, 2, \dots, n-1\}$, and that

$$\det C = (-1)^{n-1}[-1 + A_n(A_1 b_{1n} b_{n1} + A_2 b_{2n} b_{n2} + \dots + A_{n-1} b_{n-1n} b_{nn-1})].$$

This leads directly to the next practical stability result, this time expressed in terms of a single inequality.

Theorem 3.2. *There is a unique coexistence equilibrium of (9) which is globally asymptotically stable in $\text{int}(\mathbb{R}_+^n)$ provided that*

$$A_n(A_1 b_{1n} b_{n1} + A_2 b_{2n} b_{n2} + \dots + A_{n-1} b_{n-1n} b_{nn-1}) < 1.$$

To illustrate Theorem 3.2, we have represented in Fig. 2 the regions of the A_1 - A_2 parameter space that lead to a globally stable coexistence equilibrium for a 3-dimensional version of (9). For Fig. 2, $\alpha_{13} = 0.5$, $\alpha_{31} = 0.8$, $\alpha_{23} = 0.6$, $\alpha_{32} = 0.1$, while $A_3 = 0.2$ (for (a)), $A_3 = 0.6$ (for (b)), $A_3 = 1.5$ (for (c)).

3.3. Wright’s model

With a view to using our previously established stability results, let us now consider the model

$$x'_i = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + x_i \sum_{k \neq i} \frac{\beta_{ik} x_k}{\alpha_{ik} + x_k}, \quad 1 \leq i \leq n. \tag{10}$$

introduced in Georgescu et al. (2017) as a n -species version of the model proposed in Wright and simple (1989). In (10), as well as in its initial version proposed in Wright and simple (1989), both suitable to describe pollination or other foraging mutualisms, *per capita* mutualistic benefits saturate as partner density increases in a similar manner to what happens when foraging on resources due to resource handling or uptake rate. Note that in (10) the *per capita* mutualistic benefits are *a priori* bounded, regardless of partner density.

At a glance, (10) does not fit the framework (1), due to the mutualistic contribution being expressed as an increase in predation and having the “wrong” sign. Let us first restate (10) as

$$x'_i = x_i \left[\left(r_i + \sum_{j \neq i} \beta_{ij} \right) - \left(\frac{r_i x_i}{K_i} + \sum_{j \neq i} \frac{\beta_{ij} \alpha_{ij}}{\alpha_{ij} + x_j} \right) \right], \quad 1 \leq i \leq n. \tag{11}$$

In these settings,

$$a_i(x_i) = r_i + \sum_{k \neq i} \beta_{ik}, \quad f_i(x_1, x_2, \dots, x_n) = \frac{r_i x_i}{K_i} + \sum_{k \neq i} \frac{\beta_{ik} \alpha_{ik}}{\alpha_{ik} + x_k}$$

and consequently

$$\frac{a_i(s_i x)}{f_i(s_1 x, s_2 x, \dots, s_n x)} = \frac{r_i + \sum_{k \neq i} \beta_{ik}}{\frac{r_i s_i x}{K_i} + \sum_{k \neq i} \frac{\beta_{ik} \alpha_{ik}}{\alpha_{ik} + s_k x}}.$$

Note that ultimately decreases as a function of x . It then follows that

$$\mathbf{R}_i(s_1, s_2, \dots, s_n) = \lim_{x \rightarrow \infty} \frac{r_i + \sum_{k \neq i} \beta_{ik}}{\frac{r_i s_i x}{K_i} + \sum_{k \neq i} \frac{\beta_{ik} \alpha_{ik}}{\alpha_{ik} + s_k x}} = 0, \quad 1 \leq i \leq n,$$

the matrix C being then given by

$$C = -I_n,$$

which is Hurwitz stable.

Note that

$$\begin{aligned} & a_i(\alpha x) - f_i(\alpha x) > a_i(x) - f_i(x) \\ \Leftrightarrow & r_i + \sum_{k \neq i} \beta_{ik} - \left(\frac{r_i \alpha x_i}{K_i} + \sum_{k \neq i} \frac{\beta_{ik} \alpha_{ik}}{\alpha_{ik} + \alpha x_k} \right) > r_i \\ & + \sum_{k \neq i} \beta_{ik} - \left(\frac{r_i x_i}{K_i} + \sum_{k \neq i} \frac{\beta_{ik} \alpha_{ik}}{\alpha_{ik} + x_k} \right) \end{aligned}$$

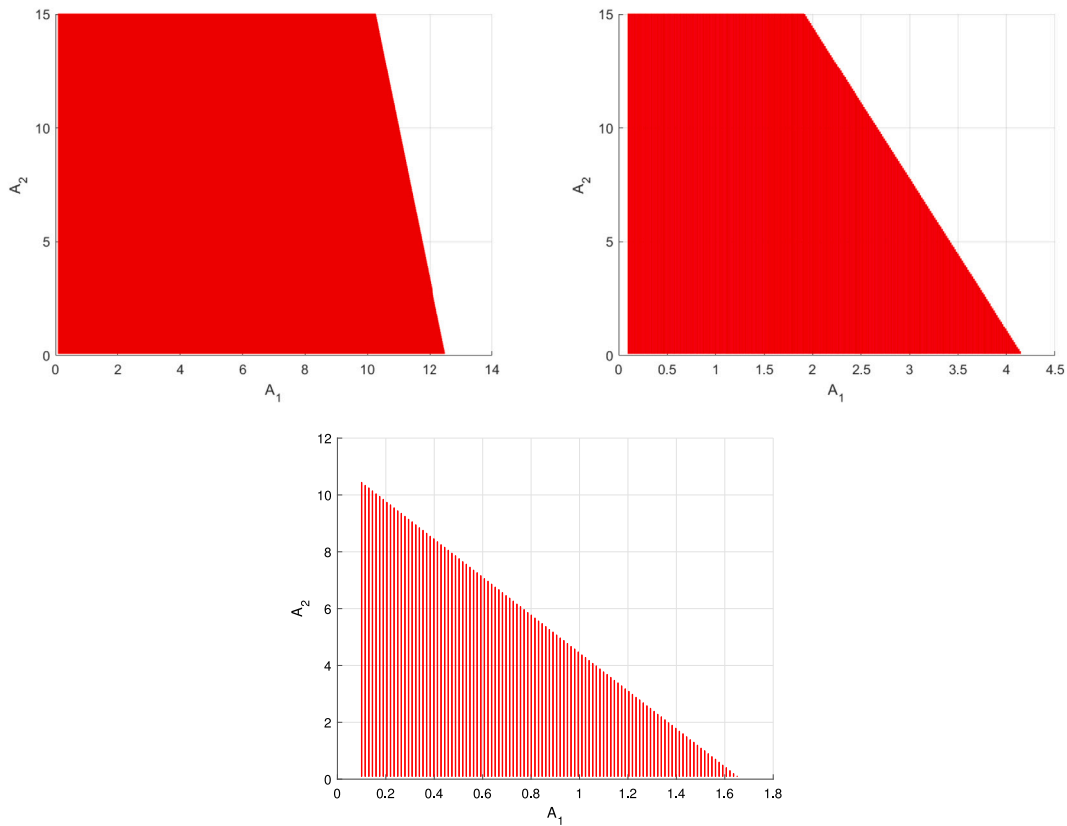


Fig. 2. Regions in the A_1 - A_2 plane leading to a globally stable coexistence equilibrium for a 3-dimensional version of (9) and distinct values of A_3 .

$$\Leftrightarrow \frac{r_i x_i}{K_i} > \sum_{k \neq i} \frac{\beta_{ik} \alpha_{ik}}{(\alpha_{ik} + x_k)(\alpha_{ik} + \alpha x_k)}$$

Since $x \gg 0$ is arbitrary, the sublinearity condition (SL) will not hold, so one cannot use Theorem 2.3 in this case. With a view towards using Theorem 2.6 instead, let us observe that

$$(D_0(x) - Df(x))_{i,j} = \begin{cases} -\frac{r_i}{K_i}, & i = j \\ \frac{\beta_{i,j} \alpha_{i,j}}{(\alpha_{i,j} + x_j)^2}, & i \neq j, \end{cases}$$

from which (H3p) follows. Also,

$$a(0) - f(0) = \text{diag}(r_i, 1 \leq i \leq n),$$

which implies that (H2p) is satisfied too. Consequently, the following result holds.

Theorem 3.3. *There is a unique coexistence equilibrium of (10) which is globally asymptotically stable in $\text{int}(\mathbb{R}_+^n)$.*

To illustrate Theorem 3.3, we have represented in Fig. 3 several trajectories of a 3-dimensional version of (10) corresponding to different initial data, all converging to the coexistence equilibrium $x^* = (233.3, 300, 499.8)$. For Fig. 3, $r_1 = 0.3, r_2 = 0.2, r_3 = 0.1, K_1 = 100, K_2 = 100, K_3 = 100, \alpha_{12} = 0.1, \alpha_{13} = 0.3, \beta_{12} = 0.1, \beta_{13} = 0.3, \alpha_{21} = 0.2, \alpha_{23} = 0.2, \beta_{21} = 0.1, \beta_{23} = 0.3, \alpha_{31} = 0.3, \alpha_{32} = 0.1, \beta_{31} = 0.1, \beta_{32} = 0.3$, the initial data being generated using Matlab's randperm function.

3.4. Graves et al.'s model

Let us now consider the model

$$x'_i = r_i x_i \left(1 - \frac{x_i}{K_i} \right) + c_i x_i \left(1 - e^{-\sum_{k \neq i} \alpha_{ik} x_k} \right), \quad 1 \leq i \leq n, \quad (12)$$

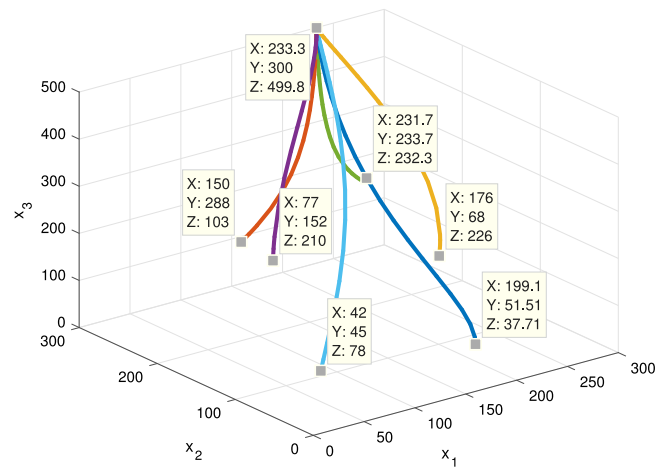


Fig. 3. Trajectories converging to a globally stable coexistence equilibrium for a 3-dimensional version of (10) and different initial data.

also introduced in Georgescu et al. (2017) as a n -species version of the model proposed in Graves et al. (2006). The (2-dimensional) model of Graves et al. (2006), updating an earlier model of Dean (1983) in order to remove singularities along certain lines in the phase space, assumes that each mutualist asymptotically enhances the others' growth rates rather than directly affecting the carrying capacity.

Called by its proponents "limited per capita growth rate mutualism model", the model of Graves et al. can accommodate facultative-facultative, facultative-obligate and obligate-obligate mutualisms (although we do require that (12) satisfies $c_i \geq 0, 1 \leq i \leq n$ and $\alpha_{ik} \geq 0, 1 \leq i, k \leq n, i \neq k$ in order to fit our facultative mutualism narrative, the original model of Graves et al. does not have this limitation), reduces

to the Gause–Witt model locally, but it is more suitable to represent strong mutualistic interactions, being used in Graves et al. (2006) to describe a lichen symbiosis composed of nitrogen-fixing cyanobacteria in symbiotic association with a fungus.

Again, at a glance, (12) does not fit our framework (1). Let us restate (12) as

$$x'_i = x_i \left[(r_i + c_i) - \left(\frac{r_i x_i}{K_i} + c_i e^{-\sum_{k \neq i} \alpha_{ik} x_k} \right) \right], \quad 1 \leq i \leq n. \quad (13)$$

In these settings,

$$a_i(x_i) = r_i + c_i, \quad f_i(x_1, x_2, \dots, x_n) = \frac{r_i x_i}{K_i} + c_i e^{-\sum_{k \neq i} \alpha_{ik} x_k}$$

and consequently

$$\frac{a_i(s_i x)}{f_i(s_1 x, s_2 x, \dots, s_n x)} = \frac{r_i + c_i}{\frac{r_i s_i}{K_i} x + c_i e^{-\left(\sum_{k \neq i} \alpha_{ik} s_k\right) x}}.$$

Note that this ultimately decreases as a function of x . It is seen that

$$\begin{aligned} \mathbf{R}_i(s_1, s_2, \dots, s_n) &= \lim_{x \rightarrow \infty} \frac{r_i + c_i}{\frac{r_i s_i}{K_i} x + c_i e^{-\left(\sum_{k \neq i} \alpha_{ik} s_k\right) x}} \\ &= 0, \quad 1 \leq i \leq n, \end{aligned}$$

the matrix C being given by

$$C = -I_n,$$

which is Hurwitz stable. Note that

$$\begin{aligned} a_i(\alpha x) - f_i(\alpha x) &> a_i(x) - f_i(x) \\ \Leftrightarrow r_i + c_i - \left(\frac{r_i \alpha x_i}{K_i} + c_i e^{-\sum_{k \neq i} \alpha_{ik} \alpha x_k} \right) &> r_i + c_i - \left(\frac{r_i x_i}{K_i} + c_i e^{-\sum_{k \neq i} \alpha_{ik} x_k} \right) \\ \Leftrightarrow \frac{r_i x_i (1 - \alpha)}{K_i} &> c_i \left(e^{-\alpha \sum_{k \neq i} \alpha_{ik} x_k} - e^{-\sum_{k \neq i} \alpha_{ik} x_k} \right). \end{aligned}$$

Again, since $x \gg 0$ is arbitrary, the sublinearity condition (SL) will not hold, so one still cannot use Theorem 2.3. Let us observe that

$$(D_0(x) - Df(x))_{i,j} = \begin{cases} -\frac{r_i}{K_i}, & i = j \\ c_i \alpha_{i,j} e^{-\sum_{k \neq i} \alpha_{ik} x_k}, & i \neq j, \end{cases}$$

from which (H3p) follows. Also,

$$a(0) - f(0) = \text{diag}(r_i, 1 \leq i \leq n),$$

which implies that (H2p) holds. Consequently, the following result holds.

Theorem 3.4. *There is a unique coexistence equilibrium of (12) which is globally asymptotically stable in $\text{int}(\mathbb{R}_+^n)$.*

To illustrate Theorem 3.4, we have represented in Fig. 4 several trajectories of a 3-dimensional version of (12) corresponding to different initial data, all converging to the coexistence equilibrium $x^* = (129.9, 110, 120)$. For Fig. 4, $r_1 = 1, r_2 = 1, r_3 = 1, c_1 = 0.3, c_2 = 0.1, c_3 = 0.2, K_1 = 100, K_2 = 100, K_3 = 100, \alpha_{12} = 0.1, \alpha_{13} = 0.3, \alpha_{21} = 0.2, \alpha_{23} = 0.2, \alpha_{31} = 0.3, \alpha_{32} = 0.1$, the initial data being generated using Matlab’s randperm function.

4. Conclusions

This paper aims at expanding the scope of the abstract framework introduced in Georgescu et al. (2017) for a discussion of generic multispecies mutualisms from the viewpoint of establishing boundedness by presenting sufficient conditions for the global stability of the coexistence equilibria. Conversely, the situation in which solutions go unbounded is also of concern, as this possibility always looms over models of mutualism.

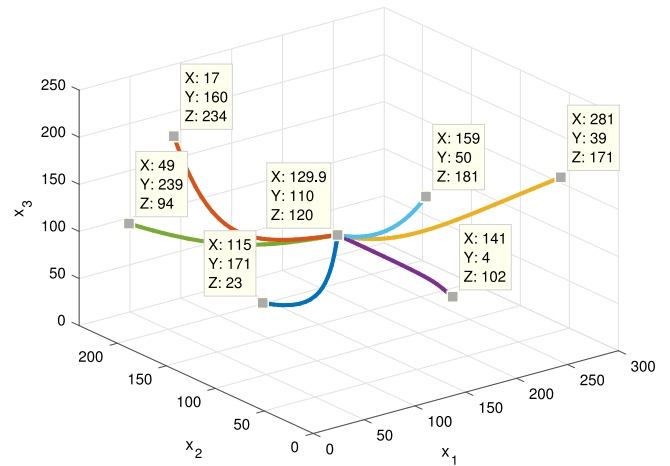


Fig. 4. Trajectories converging to a globally stable coexistence equilibrium of a 3-dimensional version of (12) and different initial data.

These conditions, involving both terms describing intrinsic growth functions and terms characterizing mutualistic interactions, are formulated in terms of reproductive numbers which are defined in a non-local manner and characterize the mutualistic support received at higher population densities. Due to the specific form of certain assumptions, our approach is applicable to the study of facultative mutualisms only. Note that in order to characterize the dynamics of the system one needs to define a reproductive number for each species, rather than use a single one for the entire model, as it is the case for disease propagation models. Of primary use are results regarding the asymptotic behavior of monotone dynamical systems that offer a trichotomy perspective.

If the reproductive numbers have a certain quasi-polynomial form motivated by the specifics of Wolin and Lawlor’s model, a single parameter can then be used to formulate a stability condition rather than multiple ones, namely the spectral abscissa of a certain matrix of coefficients. A more comprehensive investigation to delineate other situations in which the reproductive numbers aggregate as a single parameter is still needed. Our findings are then applied to establish the global asymptotic stability of the coexistence equilibria for n -species versions of several mutualistic models in current use.

Due to the plethora of mechanisms that can lead of a mutualistic interaction, our framework is, unsurprisingly, not without limitations. Particularly, due to the sign of the terms describing mutualistic interactions, our framework cannot describe a truly generic situation in which the mutualistic support leads to an increase in growth rates (although it is successful in several particular situations), a parallel approach being needed to deal with that specific type of mutualisms. In particular, our model cannot be used to discuss the stability properties of a Gause–Witt mutualism, for which the splitting and rearranging procedure involving the terms describing mutualistic interactions employed above for Wright’s and Graves et al.’s models does not function anymore (note that this procedure requires, apart from a specific form of those terms, the *a priori* boundedness of per capita mutualistic benefits).

As such, our stability results are not directly comparable with those established in Travis and Post (1979), where the stability of a n -dimensional Gause–Witt mutualistic community near a feasible equilibrium is discussed in terms of the stability of the interaction matrix evaluated at that equilibrium. By contrast, our matrix C is not localized, in the sense that it is not tied to any equilibrium in particular or to any Jacobian, and it is defined via (a specific form of) the reproductive numbers, rather than directly via the species interaction terms.

While the stability results established in Travis and Post (1979) are of a local nature, our analysis, motivated by the global stability results for 2-dimensional models of mutualism presented in Georgescu et al.

(2016), Maxin et al. (2017) and Vargas-De-León (2012), is geared towards proving global stability results instead. Thus, it is not exhaustive, as it overlooks genuine local stability considerations and it is perhaps tributary to the particular requirements of the main theoretical tools of concern, Theorems 2.1 and 2.2, and to the particular assumptions involved in the construction of our framework (as previously noted, neither the sublinearity nor the monotonicity conditions hold for all commonly used models).

Particularly, if the sublinearity condition does not hold, it is entirely possible to find multiple coexistence equilibria for models that lie within the confines of our framework, as our other assumptions do not ensure uniqueness by themselves. In this regard, an investigation on the stability of two-species models of mutualism for which birth and death are modeled as separate processes has been performed in Georgescu and Zhang (2023), delineating between accelerating (higher-powered) and decelerating (lower-powered) density dependences. It has subsequently been determined that accelerating density dependences promote the stability of coexistence equilibria, while decelerating density dependences either completely destabilize the system via promoting the unboundedness of solutions or give rise multiple coexistence equilibria.

Our settings do not accommodate models of mutualism that are derived via Levin's colonization-extinction metapopulation framework such as those of Klausmeier (2001) or Nee (2000) (note that the variables in Klausmeier (2001) and Nee (2000) represent proportions of patches, rather than population sizes, leading to undesirable signs for certain interaction terms). For similar reasons, our framework does not natively accommodate the interplay between mutualism and other types of interactions such as predation and competition either and models such as the one presented in Jelle Lever et al. (2014) are not amenable to being treated within the confines of our framework unless a splitting and rearranging procedure related to the one employed above for Wright's and Graves et al.'s models is available.

CRediT authorship contribution statement

Paul Georgescu: Writing – original draft, Investigation, Formal analysis. **Hong Zhang:** Writing – original draft, Funding acquisition.

Declaration of competing interest

The authors of the paper “*Global stability of coexistence equilibria for n-species models of facultative mutualism*”, Paul Georgescu (corresponding author) and Hong Zhang hereby declare no conflict of interest.

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