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Threshold boundedness conditions for *n*-species mutualisms

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Abstract

We establish boundedness results for a model of mutualism with an arbitrary number of species which encompasses several classic two-species models, even when extended to their respective multidimensional versions. These conditions are obtained under fairly general assumptions on the mathematical form of the functions modelling the mutualistic interactions and are expressed in terms of reproductive ratios at high population densities introduced ad hoc. We then discuss particular cases in which there is a single threshold parameter separating boundedness from unboundedness. The situation in which the unboundedness is caused by a particular subset of species is also of concern.

Keywords: mutualistic interaction, boundedness, Metzler matrices, reproductive ratios
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1. Introduction

Species within any ecosystem interact with each other in multiple, often complex, ways. Such interactions can be antagonistic, beneficial or even a combination of the two, as seen in some pollination–herbivory interactions in which the insect pollinates the plant but its larvae feed on the leaves of the same plant (Revilla and Encinas-Viso [26]).

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Due to the complexity of ecological processes, the importance of having better modeling tools is self-evident. In particular, mutualistic interactions, which lead to a net benefit for all species involved (Boucher *et al* [5]), present unique challenges due to several factors, both biological and mathematical. As mentioned in Bronstein *et al* [6], there is evidence that species interactions fostered the diversification of lineages in the past. Of these interactions, mutually beneficial partnerships are often cited to account for the rise of particular traits to ecological dominance. An example of a possibly crucial role played by a mutualism is given by a lineage of several plant species that are pollinated exclusively by a particular insect lineage. This suggest that herbivore–pollinator interaction was responsible for the diversification of both plants and insect pollinators. Nevertheless, as the authors of [6] acknowledge, it is quite difficult and rare to find empirical evidence of a particular mutualistic relationship, especially if it refers to an ancient one. This is where robust mathematical models can be used to validate or invalidate certain ecological hypotheses.

While most existing models of mutualism are bi-dimensional, ecosystems are seldom limited to groups of only two species interactions. Most plants, after all, are pollinated by more than one insect. Indeed, many existing studies on mutualistic interactions are confined to the two-species case (see, for instance, Addicott [1], Graves *et al* [10], May [20], Vargas–De–León [33], Wolin and Lawlor [36], Wright [37]), comparatively fewer being dedicated to the case of multispecies communities. This happens in spite of biological findings which demonstrate that mutualistic interactions between two species may be greatly affected by species external to the mutualism (Bacher and Friedli [2]), fact which may make the consideration of pairwise interactions without their environmental context somewhat misleading. Furthermore, multispecies mutualisms appear sometimes in unexpected and quite important circumstances. One such example is provided by reef-builiding corals, which are associated with a diverse array of microbes. Among the best known of such microbes, found in all reef-building corrals, is a class of symbionts called *zooxanthellar* (see also Knowlton and Forest [15] and references therein). For a long time considered a single species, they are now recognized as several genetically diverse groups that live in a single colony thus forming a multi-species mutualism interaction. As mentioned in [15], coral bleaching (the loss of zooxanthellae) and coral diseases, both increasing over the last decades, may be examples of mutualistic instability.

It is also worth considering that there are several possible shades of (and on) mutualisms (Bronstein *et al* [6]). For instance, in protection mutualisms, benefits are obtained only when natural enemies or detrimental conditions are present. If they are not, then the interactions between species may yield negative effects since mutualisms involve costs too. Also, some mutualisms are indirect, the positive effects being transmitted through a chain of intermediary species, whose interactions between themselves and with the mutualists may nullify in certain conditions the pairwise benefits. Symbiotic interactions may incur both benefits and costs and shift in a continuum between mutualism and parasitism, especially if one adopts the view that mutualistic interactions are essentially exploitative and one species exploits the other in order to gain a benefit (Neuhauser and Fargione [23]). Mutualistic interactions, particularly consumer-resource obligate ones such as the interaction between leaf-cutter ants and their fungus garden discussed in Kang *et al* [14], may function at different trophic levels and consequently face a trade-off in allocation of efforts towards the maintenance of the resource and towards the production and care of offsprings. To fill this vacuum, a conceptual framework for defining ecological effects in plant-animal mutualisms has been proposed in Vázquez *et al* [35].

Lately, a network perspective has been introduced to the study of mutualistic communities (Bascompte *et al* [3], Jordano *et al* [13]), being observed that mutualistic networks are often of a heterogeneous nature. That is, while most of the participating species are only involved in a couple of interactions, a few ‘privileged’ species are much more connected than the others

(Jordano *et al* [13]), one of the causes being that longer-lived species often interact with different short-lived partners at distinct stages of their lives (Palmer *et al* [24], Husband *et al* [11]).

All reasons outlined above justify the need of a framework for models of mutualism with an unspecified number of species. The focus of this paper is on defining a general class of models of mutualism in terms of consistency hypotheses introduced ad hoc and obtaining conditions for the boundedness and unboundedness of solutions, respectively, in terms of threshold parameters which are similar in scope to the basic reproduction number from mathematical epidemiology.

Our threshold parameters, however, are computed in very different conditions. That is, they are not computed in a near-extinction situation, as it is the case in mathematical epidemiology and, to a lesser extent, in ecology (Georgescu and Hsieh [9], Garrione and Rebelo [8]), but at high population densities, under given species proportionality. The reason is that, as far as the validity of the model is concerned, what is important is not the extinction of species, but their blow-up. Also, a model of mutualism has an entirely different structure, not exhibiting the asymmetry which is characteristic to disease propagation models and predator-prey models. A single threshold parameter, based on the dynamics of a single species or compartment, may consequently not be enough to describe the behavior of solutions for a model of mutualism, and we employ one reproductive ratio per species to introduce our boundedness conditions.

We also observe that for a representative class of models which includes n-dimensional versions of several two-dimensional (2D) models in common use, the boundedness condition can be expressed in terms of eigenvalues for a certain matrix of coefficients, which represents an useful algebraic test for boundedness. Establishing the boundedness of the solutions is one of the key steps in validating models of mutualism. In the case of two-species models, this is the first step toward proving the global stability of a co-existence equilibrium. For more than two species, an additional question which we address is whether only a privileged subset of them is responsible for causing an unbounded solution which, ultimately, makes the model invalid.

The paper is organised as follows. In section 2, we introduce the class of models which is of concern in this paper and state the assumptions which represent the abstract framework for its study. We then introduce our threshold parameters, called reproductive ratios, and obtain the boundedness and unboundedness conditions, respectively, in terms of those ratios. In section 3, we observe that in a particular case the boundedness condition is equivalent to the Hurwitz stability of a certain matrix of coefficients. Section 4 is devoted to the applicability of our results to several concrete models, introduced ad hoc or as n-dimensional versions of 2D models in current use. Section 5 is concerned with the case in which only a group of species (not all) are the actual cause of unboundedness. This paper ends with a section in which we put our results into a larger perspective and indicate directions of further study and with an appendix which contains a few notions of matrix theory which are necessary to state and prove our results.

2. Main results

In proving our main result we use boundedness techniques similar to those employed in [18, 19].

Consider the mutualism system

$$x_i' = x_i[a_i(x_i) - f_i(x_1, x_2, ..., x_n)], \quad 1 \leqslant i \leqslant n, \tag{1}$$

in which the functions a_i and f_i, $1 \leqslant i \leqslant n$, are assumed to be positive and continuous. First, we state several assumptions introduced ad hoc.

(L) The logistic assumption. For all $1 \leqslant i \leqslant n$, there exist $K_i > 0$ such that $a_i(K_i) - f_i(0, .., 0, K_i, 0, ...0) = 0$ and

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

(M) The mutualistic assumption. For all $1 \leqslant i \leqslant n$, $f_i(x_1, .., x_n)$ is decreasing in x_j for $j \neq i$.

(C1) Consistency assumption. For all $1 \leqslant i \leqslant n$, $f_i(x_1, ..., x_n)$ is increasing in x_i.

(C2) Consistency assumption. For all $1 \leqslant i \leqslant n$, $\frac{a_i(s_i x)}{f_i(s_1 x, ..., s_n x)}$ is eventually decreasing for all $s_i > 0$, i.e.

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

where M_i are positive real constants that may depend on $s_1, s_2, \ldots, s_n$.

Since the f_i's represent removal rates, assumption (M) represents the fact that the mutualistic support the species give to each other leads to a decrease in the death rates. Assumptions (C1) and (C2) essentially describe the effects of saturation. Also, assumption (C2) ensures that the following limits are defined:

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

It is easy to see that the $\mathcal{R}_i$'s are invariated by a scalar multiplication of all s_i's, in the sense that

$$\mathcal{R}_i(cs_1, cs_2, ..., cs_n) = \mathcal{R}_i(s_1, s_2, ..., s_n), \quad \text{for}\ c > 0.$$

Consequently, s_i, $1 \leqslant i \leqslant n$, are to be understood as characterizing relative population sizes and $\mathcal{R}_i(s_1, s_2, ..., s_n)$ characterizes the ability of species i to reproduce at high population sizes under the given species proportionality. Under the stated form of (C2), x is to be understood as a common measuring unit of all populations and does not bear an immediate biological meaning. It is true that (C2) can be stated (and later used) only for parameters s_i, $1 \leqslant i \leqslant n$ with sum 1, in which case x represents the total (of all species) population size and s_i represent the percentage held by the ith population. However, this approach has the disadvantage of lumping all species (which may or may not have similar characteristics) into a total population size, although it should also be mentioned that if the x_i's represent adimensionalized quantities, then this approach may become reasonable enough.

Also, the $\mathcal{R}_i$'s represent birth-to-death ratios, or, perhaps more aptly, growth-to-loss ratios, since a_i and f_i are only defined modulo functions of x_i and consequently a_i may or may not contain terms pertaining to the removal of species i. The $\mathcal{R}_i$'s also measure the amount of mutualistic support each species receive from the others.

From the assumptions (M) and (L), we see that the solutions of (1) with initial data in $(0, \infty) \times (0, \infty) \times \ldots \times (0, \infty)$ are bounded from below by positive constants since

$$x_i' > x_i[a_i(x_i) - f_i(0, ..., 0, x_i, 0, ..., 0)] > 0, \quad 1 \leqslant i \leqslant n,$$

for $x_i < K_i$. Consequently, the following result holds.

Theorem 2.1. *Assuming (M) and (L), the solutions of the system (1) with initial data in* $(0, \infty) \times (0, \infty) \times \ldots \times (0, \infty)$ *are bounded from below by positive constants that may depend on the initial data.*

Having noticed that $\mathcal{R}_i$'s represent growth-to-loss ratios, it is natural to expect that if the losses exceed the growths at higher population sizes, for each population on their own, then the population sizes cannot grow indefinitely, that is, remain bounded, although the boundedness constants may depend on the initial population sizes. The following result quantifies this remark.

Theorem 2.2. *Assuming (M) and (C2), if there are* $\alpha_1, \alpha_2, \dots \alpha_n > 0$ *such that*

$$\mathcal{R}_i(\alpha_1, \alpha_2, \dots, \alpha_n) < 1, \quad \text{for all } 1 \leqslant i \leqslant n,$$

then the solutions of (1) are bounded from above by positive constants that may depend on the initial data.

Proof. Let us define

$$h(t) = \max\left\{\frac{x_1(t)}{\alpha_1}, \frac{x_2(t)}{\alpha_2}, \dots, \frac{x_n(t)}{\alpha_n}\right\}.$$

Suppose that, for a given t, one has that $h(t) = \frac{x_i(t)}{\alpha_i}$, for some $1 \leqslant i \leqslant n$. Then

$$x_j(t) \leqslant \frac{\alpha_j x_i(t)}{\alpha_i} \quad \text{for } j \neq i.$$

Consequently,

$$\frac{x_i'(t)}{x_i} \leqslant f_i\left(\frac{\alpha_1 x_i}{\alpha_i}, \frac{\alpha_2 x_i}{\alpha_i}, \dots, x_i, \dots, \frac{\alpha_n x_i}{\alpha_i}\right)\left[\frac{a_i(x_i)}{f_i\left(\frac{\alpha_1 x_i}{\alpha_i}, \frac{\alpha_2 x_i}{\alpha_i}, \dots, x_i, \dots, \frac{\alpha_n x_i}{\alpha_i}\right)} - 1\right].$$

Using the variable change $x_i = \alpha_i u$, one sees that

$$\begin{aligned}\lim_{x_i \to \infty} \frac{a_i(x_i)}{f_i\left(\frac{\alpha_1 x}{\alpha_i}, \frac{\alpha_2 x}{\alpha_i}, \dots, x, \dots, \frac{\alpha_n x}{\alpha_i}\right)} &= \lim_{u \to \infty} \frac{a_i(\alpha_i u)}{f_i(\alpha_1 u, \alpha_2 u, \dots, \alpha_i u, \dots, \alpha_n u)} \\ &= \mathcal{R}_i(\alpha_1, \alpha_2, \dots, \alpha_n).\end{aligned}$$

It follows that $\frac{x_i'(t)}{x_i} < 0$ for x_i large enough. Consequently, denoting by D^+h the upper Dini derivative of h (see, for instance, Lakshmikantham and Leela [16, page 7]), one may infer that $D^+h(t) < 0$ when $h(t)$ is large enough, and consequently $h(t)$ is bounded from above. ☐

Since the system (1) is already known to be uniformly bounded from below by theorem 2.1, the boundedness of the solutions implies the existence of a positive equilibrium by theorem 2.8.6 of Bhatia and Szegö [4] (see also Smith and Waltman [30], theorem D.3). Consequently, one obtains the following result.

Corollary 2.1. *Assuming (L), (M), (C1) and (C2), if there are* $\alpha_1, \alpha_2, \dots \alpha_n > 0$ *such that*

$$\mathcal{R}_i(\alpha_1, \alpha_2, \dots, \alpha_n) < 1, \quad \text{for all } 1 \leqslant i \leqslant n,$$

then there is a positive equilibrium $\mathbf{E}^* = (x_1^*, x_2^*, \dots, x_n^*)$ *of (1).*

A converse (in some sense) result holds as well, under slightly stronger monotonicity hypotheses on the functions which appear in (C2).

Theorem 2.3. *Suppose that (C2) is replaced by*

(C2)$'$ *For all* $1 \leqslant i \leqslant n$, $\frac{a_i(s_i x)}{f_i(s_1 x, \ldots, s_n x)}$ *is decreasing as a function of* x *for all* $s_1, s_2, \ldots, s_n > 0$, *i.e.*

$$\frac{\mathrm{d}}{\mathrm{d}x}\left(\frac{a_i(s_i x)}{f_i(s_1 x, ..., s_n x)}\right) < 0 \quad \text{for} \quad x > 0.$$

If there is a positive equilibrium $\mathbf{E}^*$, *then there exist* $\alpha_1, \alpha_2, \ldots, \alpha_n > 0$ *such that*

$$\mathcal{R}_i(\alpha_1, \alpha_2, \ldots, \alpha_n) < 1, \quad \text{for all } 1 \leqslant i \leqslant n.$$

Proof. From the equilibrium relations, one sees using (C2)$'$ that

$$1 = \frac{a_i(x_i^*)}{f_i(x_1^*, x_2^*, \ldots, x_n^*)} > \frac{a_i(x_i^* x)}{f_i(x_1^* x, x_2^* x, \ldots, x_n^* x)}, \quad \text{for } x > 1, \quad 1 \leqslant i \leqslant n.$$

The conclusion follows passing to limit in the above inequality. □

If the opposite situation happens, that is, if the growths exceed the losses, then it is natural to expect that the population sizes grow unbounded.

Theorem 2.4. *Assuming (M) and (C2), if there are* $\alpha_1, \alpha_2, \ldots \alpha_n > 0$ *such that*

$$\mathcal{R}_i(\alpha_1, \alpha_2, \ldots, \alpha_n) > 1, \quad 1 \leqslant i \leqslant n,$$

then the solutions of (1) are unbounded if the initial population sizes are high enough.

Proof. Since the solutions of (1) are bounded from below by a positive constant, we can assume that there exist $\xi > 0$ such that $x_i(t) > \xi$ for all $1 \leqslant i \leqslant n$. Seeking for a contradiction, let us assume that the function

$$h(t) := \min\left\{\frac{x_1(t)}{\alpha_1}, \frac{x_2(t)}{\alpha_2}, \ldots, \frac{x_n(t)}{\alpha_n}\right\}$$

is bounded from above, i.e. $h(t) < M$ for a certain $M > 0$ and for every $t \geqslant 0$. Suppose that $h(t) = \frac{x_i(t)}{\alpha_i}$ for some fixed $1 \leqslant i \leqslant n$. Then

$$x_j(t) \geqslant \frac{\alpha_j x_i(t)}{\alpha_i} \quad \text{for } j \neq i.$$

It then follows that

$$\frac{x_i'(t)}{x_i} \geqslant f_i\left(\frac{\alpha_1 x_i}{\alpha_i}, \frac{\alpha_2 x_i}{\alpha_i}, \ldots, x_i, \ldots, \frac{\alpha_n x_i}{\alpha_i}\right)\left[\frac{a_i(x_i)}{f_i\left(\frac{\alpha_1 x_i}{\alpha_i}, \frac{\alpha_2 x_i}{\alpha_i}, \ldots, x_i, \ldots, \frac{\alpha_n x_i}{\alpha_i}\right)} - 1\right]$$

$$\rangle f_i(\alpha_1 M, ..., \alpha_{i-1} M, \xi, \alpha_{i+1} M, ..., \alpha_n M)\left[\frac{a_i(x_i)}{f_i\left(\frac{\alpha_1 x_i}{\alpha_i}, \frac{\alpha_2 x_i}{\alpha_i}, \ldots, x_i, \ldots, \frac{\alpha_n x_i}{\alpha_i}\right)} - 1\right].$$

Using the same change of variable as in the previous theorem and assuming that the initial condition satisfies $x_i(0) > M_i$, passing to limit in the above expression one obtains

$$\frac{x_i'}{x_i} > f_i(\alpha_1 M, ..., \alpha_{i-1} M, \xi, \alpha_{i+1} M, ..., \alpha_n M)[\mathcal{R}_i(\alpha_1, ..., \alpha_n) - 1] > 0.$$

This shows that h'/h is bounded from below by a positive constant m, where

$$m := \min_{1 \leqslant i \leqslant n} \{f_i(\alpha_1 M, ..., \alpha_{i-1} M, \xi, \alpha_{i+1} M, ..., \alpha_n M)[\mathcal{R}_i(\alpha_1, ..., \alpha_n) - 1]\}$$

and provided that

$$h(0) > \max_{1 \leqslant i \leqslant n} \left\{ \frac{M_i}{\alpha_i} \right\}.$$

Using this lower bound and a consequence of the Lebesgue theorem ([29, corollary 4, page 113]) we obtain

$$\ln h(t) - \ln h(0) \geqslant \int_0^t \frac{h'(\tau)}{h(\tau)} \mathrm{d}\tau > \int_0^t m \mathrm{d}\tau = mt.$$

Letting $t \to \infty$ in the above inequality it follows that $h(t) \to \infty$, contradicting our assumption that h is bounded above. Hence h and, therefore, x_i are also unbounded if the population sizes are high enough. □

3. Particular growth conditions

Let us suppose that the $\mathcal{R}_i$'s are given in the following particular form.

$$\mathcal{R}_i(s_1, s_2, \ldots, s_n) = \sum_{j=1, j \neq i}^{n} C_{ij} \left(\frac{s_j}{s_i} \right)^p, \quad 1 \leqslant i \leqslant n, \tag{2}$$

with

$$C_{ij} \geqslant 0 \quad \text{for all } 1 \leqslant i \neq j \leqslant n.$$

Then the boundedness conditions

$$\mathcal{R}_i(\alpha_1, \alpha_2, \ldots, \alpha_n) < 1, \quad 1 \leqslant i \leqslant n,$$

reduce to

$$\sum_{j=1, j \neq i}^{n} C_{ij} v_j - v_i < 0, \quad 1 \leqslant i \leqslant n,$$

with $v_i = \alpha_i^p, 1 \leqslant i \leqslant n$. This means that the vector $v = (v_1, v_2, \ldots, v_n)^T$ verifies

$$Cv \ll 0,$$

where C is the Metzler matrix given by

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

With the same notations, the unboundedness conditions reduce to

$$Cv \gg 0.$$

Using then lemmas A.1 and A.2, one obtains the following result.

Theorem 3.1. *Suppose that the growth conditions (2) are satisfied. The following properties hold true, the matrix C being defined in (3).*

- (*a*) *All solutions of (1) are bounded if and only if C is Hurwitz stable.*
- (*b*) *If C is Hurwitz unstable and irreducible, then (1) has unbounded solutions.*

Let us now suppose that the $\mathcal{R}_i$'s are given in the exponential form.

$$\mathcal{R}_i(s_1,s_2,\dots,s_n)=M_i\exp\left(-\frac{s_i^p}{\sum_{j=1,j\neq i}^n d_{ij}s_j^p}\right),\quad 1\leqslant i\leqslant n, \tag{4}$$

with

$$M_i>0, d_{ij}\geqslant 0 \quad \text{for all } 1\leqslant i\neq j\leqslant n.$$

Via similar considerations, one then arrives at the following Metzler matrix of interest

$$D=\begin{pmatrix} -1 & d_{12}\ln M_1 & \dots & d_{1n}\ln M_1 \\ d_{21}\ln M_2 & -1 & \dots & d_{2n}\ln M_2 \\ \vdots & \vdots & & \vdots \\ d_{n1}\ln M_n & d_{n2}\ln M_2 & \dots & -1 \end{pmatrix}. \tag{5}$$

which may replace C in the statement of theorem 3.1.

4. Particular cases

In this section we provide several particular cases of n-species mutualism where the bounding theorem from the previous section can be applied.

4.1. Mutualism as reduction of mortality for the benefiting species

Let us consider the model

$$x_i'=r_ix_i\left[A_i-\frac{x_i^p}{K_i+\sum_{j\neq i}b_{ij}x_j^p}\right],\quad 1\leqslant i\leqslant n,\quad p>0, \tag{6}$$

introduced here as an immediate extension of the model considered in Wolin and Lawlor [36] and May [20], which can be obtained from (6) for $n=2$ and $p=1$. Here, 'reduction of losses' means that the mutualism acts towards a reduction of the negative term, although the derivation of the model in [36] assumes that it is the birth rate that is affected by the mutualistic interaction. Actually, this model is the one which motivated us to analyse the first set of particular growth conditions given in the previous section and generally lead us to the considerations given in this paper. For this model, it is seen that

$$a_i(x_i) = r_i A_i, \quad f_i(x_1, x_2, \ldots, x_n) = \frac{r_i x_i^p}{K_i + \sum_{j\neq i} b_{ij} x_j^p}$$

and consequently

$$\frac{a_i(s_i x)}{f_i(s_1 x, s_2 x, \ldots, s_n x)} = A_i \left[\frac{K_i}{(s_i x)^p} + \sum_{j\neq i} b_{ij} \left(\frac{s_j}{s_i} \right)^p \right].$$

It then follows that

$$\mathcal{R}_i(s_1, s_2, \ldots, s_n) = A_i \left[\sum_{j\neq i} b_{ij} \left(\frac{s_j}{s_i} \right)^p \right],$$

the corresponding matrix C being given by

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

For $n = 2$, the model (6) reduces to the following model:

$$\begin{cases} x_1' &= r_1 x_1 \left(A_1 - \frac{x_1^p}{K_1 + b_{12} x_2^p} \right), \\ x_2' &= r_2 x_2 \left(A_2 - \frac{x_2^p}{K_2 + b_{21} x_1^p} \right). \end{cases} \tag{7}$$

Since in this case $C = \begin{pmatrix} -1 & A_1 b_{12} \\ A_2 b_{21} & -1 \end{pmatrix}$, its leading principal minors being

$$\Delta_1 = -1, \quad \Delta_2 = 1 - A_1 A_2 b_{12} b_{21},$$

it follows that the solutions of (7) are bounded provided that $A_1 A_2 b_{12} b_{21} < 1$. This condition ensures not only the boundedness of the solutions (and, as seen above, the existence of the positive equilibrium), but also the global stability of the positive equilibrium, via the use of the Dulac criterion (see, for instance, Martcheva [17, page 55]).

Let us now suppose that (6) has a 'privileged' species, the nth one, which interacts with all other, while species $1, 2, \ldots, n-1$ interact with species n, but do not interact with each other (see Vargas–De–León [34] for a related model). An usual example is provided by plant–pollinators systems where the species interaction may form a bi-partite graph (i.e. insects interact with plants but not among themselves). The example below represents a subset of this network focused on one insect (the privileged species) that pollinates multiple plant species. In some cases plants do depend on only one single pollinator as is the case with certain orchid species that are exclusively pollinated by the male orchid bee (see also Ramirez [28] and references therein). In this case, the model (6) reduces to

$$\begin{cases} x_1' = r_1 x_1 \left(A_1 - \frac{x_1^p}{K_1 + b_{1n} x_n^p} \right), \\ x_2' = r_2 x_2 \left(A_2 - \frac{x_2^p}{K_2 + b_{2n} x_n^p} \right), \\ \vdots \\ x_n' = r_n x_n \left(A_n - \frac{x_n^p}{K_n + b_{n1} x_1^p + \ldots + b_{nn-1} x_{n-1}^p} \right) \end{cases} \tag{8}$$

and consequently

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

Since

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

the other leading minors of order p, $1 \leqslant p \leqslant n-1$, being equal to $(-1)^p$, one finds that the bounding condition is in this case

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

A similar matrix results from another model where the threshold conditions involve logarithms. The model is somewhat artificial, i.e. biologically feasible but not immediately related to any known species interaction. Its purpose, is to show that the bounding conditions do not restrict the $\mathcal{R}_i$'s to the quasi-polynomial format given in (2).

$$\begin{cases} x_1' = r_1 x_1 \left[m_1 - K_1 \frac{x_1}{1+x_1} \left(1 + \frac{1}{1+b_1 x_n}\right)^{x_1} \right], \\ x_2' = r_2 x_2 \left[m_2 - K_2 \frac{x_2}{1+x_2} \left(1 + \frac{1}{1+b_2 x_n}\right)^{x_2} \right], \\ \vdots \\ x_n' = r_n x_n \left[m_n - K_n \frac{x_n}{1+x_n} \left(1 + \frac{1}{1+c_1 x_1 + c_2 x_2 + \dots + c_{n-1} x_{n-1}}\right)^{x_n} \right] \end{cases} \tag{9}$$

with $m_i > K_i, 1 \leqslant i \leqslant n$.

It follows that

$$\mathcal{R}_i(s_1, s_2, \dots, s_n) = \frac{m_i}{K_i} \exp\left(-\frac{s_i}{b_i s_n}\right), \text{ for } 1 \leqslant i \leqslant n-1, \text{and}$$

$$\mathcal{R}_n(s_1, s_2, \dots, s_n) = \frac{m_n}{K_n} \exp\left(-\frac{s_n}{c_1 s_1 + c_2 s_2 + \dots + c_{n-1} s_{n-1}}\right).$$

The matrix D becomes

$$D = \begin{pmatrix} -1 & 0 & \dots & 0 & b_1 \ln\left(\frac{m_1}{K_1}\right) \\ 0 & -1 & \dots & 0 & b_2 \ln\left(\frac{m_2}{K_2}\right) \\ \vdots & & & & \\ 0 & 0 & \dots & -1 & b_{n-1} \ln\left(\frac{m_{n-1}}{K_{n-1}}\right) \\ c_1 \ln\left(\frac{m_n}{K_n}\right) & c_2 \ln\left(\frac{m_n}{K_n}\right) & \dots & c_{n-1} \ln\left(\frac{m_{n-1}}{K_{n-1}}\right) & -1 \end{pmatrix}.$$

Similar to the previous example, the bounding condition becomes

$$\ln\left(\frac{m_n}{K_n}\right)\left[b_1c_1\ln\left(\frac{m_1}{K_1}\right)+b_2c_2\ln\left(\frac{m_2}{K_2}\right)\ldots+b_{n-1}c_{n-1}\ln\left(\frac{m_{n-1}}{K_{n-1}}\right)\right]<1$$

or, in a more compact form,

$$\ln\left(\frac{m_n}{K_n}\right)\ln\left[\left(\frac{m_1}{K_1}\right)^{b_1c_1}\left(\frac{m_2}{K_2}\right)^{b_2c_2}\ldots\left(\frac{m_{n-1}}{K_{n-1}}\right)^{b_{n-1}c_{n-1}}\right]<1.$$

4.2. Mutualism as a positive contribution to the fertiliy rate of the benefiting species

The following model with restricted growth rates

$$\begin{aligned} x_1' &= r_1x_1\left(1-\tfrac{x_1}{K_1}\right)+c_1x_1(1-\mathrm{e}^{-\alpha_2x_2}) \\ x_2' &= r_2x_2\left(1-\tfrac{x_2}{K_2}\right)+c_2x_2(1-\mathrm{e}^{-\alpha_1x_1}), \end{aligned} \tag{10}$$

has been proposed by Graves *et al* in [10]. From a qualitative viewpoint, the model (10), unlike the model (6), assumes that each species enhances the growth rate of the other without affecting its carrying capacity.

In what follows, we shall consider its multispecies version given by

$$x_i'=r_ix_i\left(1-\frac{x_i}{K_i}\right)+c_ix_i\left(1-\mathrm{e}^{-\sum_{j\neq i}\alpha_{ij}x_j}\right),\quad 1\leqslant i\leqslant n. \tag{11}$$

Let us first rearrange (11) in the form

$$x_i'=x_i\left[(r_i+c_i)-\left(\frac{r_ix_i}{K_i}+c_i\mathrm{e}^{-\sum_{j\neq i}\alpha_{ij}x_j}\right)\right],\quad 1\leqslant i\leqslant n. \tag{12}$$

For this model, it is seen that

$$a_i(x_i)=r_i+c_i,\quad f_i(x_1,x_2,\ldots,x_n)=\frac{r_ix_i}{K_i}+c_i\mathrm{e}^{-\sum_{j\neq i}\alpha_{ij}x_j}$$

and consequently

$$\frac{a_i(s_ix)}{f_i(s_1x,s_2x,\ldots,s_nx)}=\frac{r_i+c_i}{\frac{r_is_i}{K_i}x+c_i\mathrm{e}^{-\left(\sum_{j\neq i}\alpha_{ij}s_j\right)x}},$$

which is eventually decreasing. It then follows that

$$\mathcal{R}_i(s_1,s_2,\ldots,s_n)=0,\quad 1\leqslant i\leqslant n,$$

the corresponding matrix C being given by

$$C=-I_n,$$

which is Hurwitz stable. This ensures the boundedness of the solutions of (12) via theorem 3.1.

The following model of mutualism incorporating handling of the mutualistic partner y

$$x'=x\left[r(1-cx)+\frac{\beta y}{\alpha+y}\right]$$

has been proposed in Wright [37]. After some renotations, let us consider its multispecies version given by

$$x_i' = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + x_i \sum_{j \neq i} \frac{\beta_{ij} x_j}{\alpha_{ij} + x_j}, \quad 1 \leqslant i \leqslant n. \tag{13}$$

One may remark that this multispecies version is related to the models considered in Jelle Lever *et al* [12] and Rohr *et al* [27], the differences being that no competition terms are considered and there is no functional distinction between two categories of species (plants and pollinators in [12], plants and animals in [27]). Lastly, our model (13), unlike the model in [12], assumes that there is no immigration.

Let us first rearrange (13) in the form

$$x_i' = x_i \left[(r_i + \sum_{j \neq i} \beta_{ij}) - \left(\frac{r_i x_i}{K_i} + \sum_{j \neq i} \frac{\beta_{ij} \alpha_{ij}}{\alpha_{ij} + x_j} \right) \right], \quad 1 \leqslant i \leqslant n. \tag{14}$$

For this model, it is seen that

$$a_i(x_i) = r_i + \sum_{j \neq i} \beta_{ij}, \quad f_i(x_1, x_2, \ldots, x_n) = \frac{r_i x_i}{K_i} + \sum_{j \neq i} \frac{\beta_{ij} \alpha_{ij}}{\alpha_{ij} + x_j}$$

and consequently

$$\frac{a_i(s_i x)}{f_i(s_1 x, s_2 x, \ldots, s_n x)} = \frac{r_i + \sum_{j \neq i} \beta_{ij}}{\frac{r_i s_i x_i}{K_i} + \sum_{j \neq i} \frac{\beta_{ij} \alpha_{ij}}{\alpha_{ij} + s_j x_j}},$$

which is eventually decreasing. It then follows that

$$\mathcal{R}_i(s_1, s_2, \ldots, s_n) = 0, \quad 1 \leqslant i \leqslant n,$$

the corresponding matrix C being given by

$$C = -I_n,$$

which is Hurwitz stable. This, again, ensures the boundedness of the solutions of (14) via theorem 3.1.

Let us now observe that (13) includes the versions without competition of the models of mutualism in [12] and [27] (for [27], also without immigration), the functional distinction being a matter of setting the appropriate β_{ij}'s equal to 0. Via a comparison argument, one may see that the solutions of the models in [12] and [27] are bounded if one discounts immigration, which is not surprising, since both are models with limited per capita benefits from the mutualism.

As a consequence, it is seen that our boundedness results can be applied not only for mutualisms which act by reducing removal rates, such as (6), but also for mutualisms which enhance growth rates, although, at a glance, the particular form of our system (1) seems to tell otherwise.

5. Which species is responsible for unboundedness?

In the examples analysed in the previous section, the n conditions used in the bounding theorems actually reduced to a single threshold quantity, the spectral abscissa of a given matrix, which successfully separated boundedness from unboundedness. A natural question to ask is whether the limits $\mathcal{R}_i$ have separate roles in the bounding conditions or, from a biological perspective, whether the outcome (bounded versus unbounded) is the responsibility of the mutualistic interaction of all species together. In this section we argue that, with some additional hypotheses, one can show that the above results can be caused by a subset of the species in the system. This may be important since, when one tries to develop a realistic model of mutualism, the attention can be restricted only to the species likely to produce an unbounded solution.

Let us assume that the n species are split into two subgroups: group 1 made of $x_1,...,x_m$ on one hand and group 2 made of $x_{m+1},...,x_n$ on the other, with $m < n$. Further, suppose that group 1 gets most of its mutualistic benefits within their own group while group 2 experiences an upper bound on the mutualistic benefits from group 1. This can be expressed in the following additional hypotheses

$$\begin{aligned} f_i(x_1,...,x_m,x_{m+1},...,x_n) &\leqslant g_i(x_1,...,x_m), & 1 \leqslant i \leqslant m, \\ f_i(x_1,...,x_m,x_{m+1},...,x_n) &\geqslant h_i(x_{m+1},..,x_n), & m+1 \leqslant i \leqslant n, \end{aligned}$$

the functions g_i and h_i being assumed to satisfy the same hypotheses assumed for f_i in the previous theorems. Then we shall define

$$\mathcal{R}_i(s_1,s_2,...,s_m) := \lim_{x\to\infty} \frac{a_i(s_i x)}{g_i(s_1 x, s_2 x,...,s_m x)}, \quad 1 \leqslant i \leqslant m,$$

and

$$\mathcal{R}_i(s_{m+1},s_{m+2},...,s_n) := \lim_{x\to\infty} \frac{a_i(s_i x)}{h_i(s_{m+1} x, s_{m+2} x,...,s_n x)}, \quad m+1 \leqslant i \leqslant n.$$

The following result shows that only a subset of the total number of species experience unbounded growth, while the others decidedly do not.

Theorem 5.1. *Assuming (C1) and (C2) for the functions* g_i *and* h_i*, if there are* $\alpha_1, \alpha_2, \dots \alpha_m > 0$ *such that*

$$\mathcal{R}_i(\alpha_1,\alpha_2,\dots,\alpha_m) > 1, \quad 1 \leqslant i \leqslant m,$$

and there are $\alpha_{m+1},\alpha_{m+2},\dots,\alpha_n > 0$ *such that*

$$\mathcal{R}_i(\alpha_{m+1},\alpha_{m+2},\dots,\alpha_n) < 1, \quad m+1 \leqslant i \leqslant n,$$

then $x_1,...,x_m$ *are unbounded if the initial population sizes are high enough while* $x_{m+1},...,x_n$ *remain bounded.*

Proof. The proof is very similar to the ones presented for the bounding theorems. We only emphasize here the main difference. For the first m species, one may consider

$$h(t) = \min\left\{\frac{x_1(t)}{\alpha_1}, \frac{x_2(t)}{\alpha_2}, \dots, \frac{x_m(t)}{\alpha_m}\right\}.$$

Furthermore

$$\frac{x_i'}{x_i} = a_i(x_i) - f_i(x_1,...,x_m,x_{m+1},...,x_n) \geqslant a_i(x_i) - g_i(x_1,..,x_m), \quad 1 \leqslant i \leqslant m$$

after which the proof follows the steps from the proof of theorem 2.4. To show that the remaining species are bounded, one can define

$$h(t) = \max\left\{\frac{x_{m+1}(t)}{\alpha_{m+1}}, \frac{x_{m+2}(t)}{\alpha_{m+2}}, \ldots, \frac{x_n(t)}{\alpha_n}\right\}$$

and use the fact that

$$\frac{x_i'}{x_i} = a_i(x_i) - f_i(x_1, ..., x_m, x_{m+1}, ..., x_n) \leqslant a_i(x_i) - h_i(x_{m+1}, .., x_n), \quad m+1 \leqslant i \leqslant n,$$

after which the steps are the same as those from the proof of theorem 2.2. □

To illustrate the above considerations, let us discuss the dynamics of the following model

$$\begin{cases} x_1' = r_1 x_1 \left(A_1 - \frac{x_1^p}{K_1 + b_{12} x_2^p + b_{13} x_3^p}\right), \\ x_2' = r_2 x_2 \left(A_2 - \frac{x_2^p}{K_2 + b_{21} x_1^p + b_{23} x_3^p}\right), \\ x_3' = r_3 x_3 \left[A_3 - \left(1 + \frac{x_3^p}{K_3 + b_{31} x_1^p + b_{32} x_2^p}\right) x_3\right] \end{cases}, \tag{15}$$

with

$$p > 0, \quad b_{ij} \geqslant 0, \quad A_1 A_2 b_{12} b_{21} > 1.$$

It is seen that

$$x_1' \geqslant r_1 x_1 A_1 - \frac{r_1 x_1^{p+1}}{K_1 + b_{12} x_2^p}, \quad x_2' \geqslant r_2 x_2 A_2 - \frac{r_2 x_2^{p+1}}{K_2 + b_{21} x_1^p}$$

with

$$g_1(x_1, x_2) = \frac{r_1 x_1^{p+1}}{K_1 + b_{12} x_2^p}, \quad g_2(x_1, x_2) = \frac{r_2 x_2^{p+1}}{K_2 + b_{21} x_1^p}.$$

Also,

$$x_3' \leqslant r_3 x_3 A_3 - r_3 x_3^2,$$

with

$$h_3(x_3) = r_3 x_3^2.$$

Then

$$\mathcal{R}_1(s_1, s_2) = A_1 b_{12} \left(\frac{s_2}{s_1}\right)^p, \quad \mathcal{R}_2(s_1, s_2) = A_2 b_{21} \left(\frac{s_1}{s_2}\right)^p, \quad \mathcal{R}_3(s_3) = 0.$$

If $A_1 A_2 b_{12} b_{21} > 1$, there are $\alpha_1, \alpha_2 > 0$ such that $\mathcal{R}_1(\alpha_1, \alpha_2) > 1$, $\mathcal{R}_2(\alpha_1, \alpha_2) > 1$. From theorem 5.1 (or revisiting the considerations of section 2), it then follows by a comparison argument that x_3 remains bounded, while x_1 and x_2 grow unbounded (actually, for all initial population sizes).

Apart from helping to an easier identification of the 'troublesome' (i.e. likely to cause unboundedness) species, theorem 5.1 shows that $\mathcal{R}_i$'s may also have predictive power on their own (rather than only in association with the other $\mathcal{R}_i$'s, as theorems 2.2 and 2.4 may lead one to believe), although, naturally, they may predict only the dynamics of the species they are computed for.

6. Conclusions

Any population model, even if mathematically correct, needs to have further restrictions imposed on its solutions in order to be biologically feasible. Positively invariance of solutions is, of course, the most basic of them. Boundedness of solutions is also necessary for long term predictions in an environment of limited resources (i.e. the logistic assumption). For cooperative models, some sort of limitation of mutualistic effects is also necessary for obvious reasons. Without it, one can have what is colloquially called *the orgy of mutual benefactions* (May [20]) in which the mutualistic benefits reinforce each other *ad infinitum*.

In this paper we provided several results concerning the boundedness of solutions for a generic multi-species model of mutualism, which represents an extension to the existing literature on their two-species version. These results are stated in terms of reproductive ratios at high population densities for given relative population sizes. Our reproductive ratios are growth-to-loss ratios, however, and do not follow the classical 'sum over all age classes of fertility times survival' definition.

An open question that is a natural follow-up of this research concerns a minimal set of conditions (more general than those employed in theorem 3.1) under which the boundedness/unboundedness dichotomy is characterized by a single threshold parameter, rather by n $\mathcal{R}_i$'s. In this regard, the next generation approach of van den Driessche and Watmough [32], while successfully deriving basic reproduction numbers for disease propagation models, targets another problem (stability), the threshold parameter being computed around the relevant equilibrium (the disease-free equilibrium). Now, there is no equilibrium to work with (since boundedness is not a notion to be defined around one), and any relevant threshold should consequently have a global appeal.

Our reproductive ratios, the $\mathcal{R}_i$'s are, in some sense, volatile quantities. They are computed for given relative population ratios, which are subject to immediate change. That is, they characterize only certain instances of the model, rather than the model itself, their interplay potentially leading to rich dynamics. In this regard, a natural question is what happens with the relative population sizes when all population sizes grow unbounded. More precisely, conditions under which an 'equilibrium' is reached (that is, the relative sizes tend to stabilize) may be of interest, albeit a theoretical one. Conversely, although a competitive exclusion principle cannot hold in the classical sense, it may be of interest to see whether or not a mutualist may still 'win' by driving the others into 'relative extinction'.

Another question concerns reasonably minimal sets of conditions to guarantee the existence and global stability of the co-existence equilibrium, respectively, since several global stability results already proven for two-species mutualistic models actually assume *a priori* the existence of such steady state. In our settings, the co-existence equilibrium is obtained via the use of Brouwer fixed point theorem, which does not ensure uniqueness. Uniqueness might require stronger conditions on functions a_i and f_i appearing in (1), as strict monotonicity component-wise does not appear to suffice.

We emphasise that there will always be limitations due to the fact that there is no general form of a mutualistic model. In particular, our settings do not include any model of mutualism derived within the modelling framework of Levin's colonization-extinction metapopulation model, such as those of Nee [21] (evolution of coviruses) and Nee *et al* [22] (plant-pollinator), due to the sign pattern of the interaction terms. However, in both [21] and [22], the variables represent proportions of patches, not population sizes or densities, leading to constant total size models. That is, for the models presented in [21, 22], boundedness is, in some sense, already built-in and does not need to be studied separately.

The dynamics of a general model of a mutualistic interaction has been considered in Travis and Post [31] from a stability viewpoint. In [31], the interaction matrix is evaluated at a feasible equilibrium, the stability of the mutualistic community being then expressed in terms of the stability of the interaction matrix. Their stability considerations are then extended to communities with a limited amount of competition and a brief, conceptual discussion on the boundedness of 2D mutualisms is given. Our results are not directly comparable to those in [31], since our focus is on boundedness (specifically, on boundedness in terms of threshold parameters), rather than on stability. Also, note that our matrix C is, in some sense, a limiting quantity, being defined in terms of $\mathcal{R}_i$'s, and is not tied to any particular equilibrium or to any Jacobian.

Our model is tailored, at least formally, to represent situations in which the mutualism decreases the mortality of the benefitting species. Although section 4.2 treats the situation in which the mutualism increases fertility rates, the treatment is done by splitting the growth rates for all species and rearranging the resulting terms so that the rearranged model is formally equivalent to a mortality decreasing mutualism, that is, it relies on the particularities of the model, rather than proposes a systematic approach. A distinct framework can be introduced to represent the situation in which the mutualism increases the fertility rates in a more general manner, and we plan to do so in a forthcoming paper. Also, a worthwhile extension would be to consider abstract frameworks for multigroup models of mutualism and for the interplay between mutualisms and other interactions such as predation and competition. This would allow for a better treatment of models such as those discussed in Jelle Lever *et al* [12] and Rohr *et al* [27], which can only be treated in the framework of this manuscript using a comparison argument which involves discarding the competition part, which leads to the boundedness results not being optimal.

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Appendix. Metzler matrices

We summarise a few matrix theory notions which describe specific properties of Metzler matrices used in proving our results.

For given matrices A, B, we shall write $A \leqslant (\geqslant) B$ if $a_{ij} \leqslant (\geqslant) b_{ij}$ for all i, j and $A \ll (\gg) B$ if $a_{ij} < (>) b_{ij}$ for all i, j. A square matrix A will be called a Metzler matrix if it has nonnegative off-diagonal entries, that is, $a_{ij} \geqslant 0$ for all $i \neq j$. For a square matrix A, we shall denote the spectrum of A by $\sigma(A)$ and the spectral abscissa of A by $\mu(A)$, defined as

$$\mu(A) = \max\left\{\Re(\lambda); \lambda \in \sigma(A)\right\}.$$

We shall subsequently say that a square matrix A is Hurwitz stable if $\mu(A) < 0$, while A will be called Hurwitz unstable if $\mu(A) > 0$. The following lemma states several characteristic properties of a certain class of Metzler matrices.

Lemma A.1 ([25], Theorem 2.1). *Let A be a $n \times n$ Metzler matrix with negative elements on its diagonal. Then the following conditions are equivalent.*

1. *A is Hurwitz stable.*
2. *The leading principal minors of A are such that the sign of the ith principal minor is $(-1)^i$, $1 \leqslant i \leqslant n$.*
3. *There is a vector $v \gg 0$ such that $Av \ll 0$.*

A square matrix A is called reducible if there is a permutation matrix P such that PAP^T is a block upper triangular matrix, that is

$$PAP^T = \begin{pmatrix} M_{11} & M_{12} \\ O & M_{22} \end{pmatrix},$$

with M_{11}, M_{22} square matrices of nonzero size. A square matrix A is then called irreducible if it is not reducible. Equivalently, a $n \times n$ matrix A, $n \geqslant 2$, is irreducible if for any proper subset M of $\{1, 2, \ldots, n\}$ there are $i \in M$ and $j \in \{1, 2, \ldots, n\} \setminus M$ such that $a_{ij} \neq 0$.

Let us now indicate several further properties of Metzler matrices.

Lemma A.2 ([7], Theorem 17). *Let A be a irreducible Metzler matrix. The following properties hold.*

1. *$\mu(A) \in \sigma(A)$.*
2. *There is a vector $v \gg 0$ such that $Av = \mu(A)v$.*

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