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To cite this article: Hamlet Castillo-Alvino & Marcos Marva (2020) The competition model with Holling type II competitive response to interfering time, Journal of Biological Dynamics, 14:1, 222-244, DOI: [10.1080/17513758.2020.1742392](https://doi.org/10.1080/17513758.2020.1742392)

To link to this article: <https://doi.org/10.1080/17513758.2020.1742392>



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Published online: 08 Apr 2020.



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The competition model with Holling type II competitive response to interfering time

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ABSTRACT

In Nature, species coexistence is much more frequent than what the classical competition model predicts, so that scientists look for mechanisms that explain such a coexistence. We revisit the classical competition model assuming that individuals invest time in competing individuals of the other species. This assumption extends the classical competition model (that becomes a particular case of the model presented) under the form of a Holling type II term, that we call *competitive response to interfering time*. The resulting model expands the outcomes allowed by the classical model by (i) enlarging the range of parameter values that allow coexistence scenarios and (ii) displaying dynamical scenarios not allowed by the classical model: namely, bi-stable conditional coexistence in favour of i (either species coexist or species i wins) or tri-stable conditional coexistence (either species coexist or any of them goes extinct), being exclusion in both cases due to priority effects.

ARTICLE HISTORY

Received 26 April 2019
Accepted 27 January 2020

KEYWORDS

Interference competition;
competitive response;
interfering time

2010 MATHEMATICS

SUBJECT

CLASSIFICATIONS

34A34; 34C60

1. Introduction

The structure of ecosystems is determined by the interaction between biotic and abiotic elements. Species competition is among the most important biotic factors; individuals compete almost everywhere with individuals of the same species (intra-species competition) and/or individuals of a different species (inter-species competition).

The early theory of competition spinned around the works of Lotka, Volterra and Gause. Namely, Lotka and Volterra [23,35] found that coexistence is possible when intra-species competition is stronger than inter-species competition. The Competitive exclusion principle set by Gause [13] stated that two species occupying the same niche cannot coexist [15]. This theoretical framework is at odds with reality, given that species coexist much more often than expected within this framework [30,33,36].

Different explanations and mechanism have been proposed to explain why species coexistence is more prevalent than species exclusion. From the above referred framework, that means to describe mechanisms reducing inter-species competition (see [38] and references quoted there). For instance, in [2] extensions of the competitive exclusion principle were

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proposed. The classical niche theory [21,24] assumes that differences among two species in the use of available resource types entail a reduction in the per capita competitive effects of the two species on each other. Species dispersal strategies and habitat heterogeneity [3,25,29], the resolution at which resources are perceived by each competing species [33], the so-called equalizing and stabilizing mechanisms (a trend to minimize in average differences in species fitness or to increase negative intra-species interactions relative to negative inter-species interactions, respectively) [10], host-specific pest-based mechanism [8,16,37] or age-structure and distance between colonies [6].

The above-mentioned mechanisms focus on species strategies or environmental constraints. An alternative approach consists on focusing on the actual way competition takes place. Despite of its importance, the classical Lotka–Volterra model was somehow oversimplifying. This model assumes that species are perfectly mixed and that the effect of one species on the other is linear to the population size of its competitor [30,38]. However, [5,34] empirically shown that competitive effects can be density-dependent which entails that the nullclines, the zero growth curves of the corresponding differential or difference equations system, are non-linear in contrast to the linear nullclines of the classical Lotka–Volterra competition model. Subsequently, Nunney [30] argued that it is more interesting to focus on the nullclines curvature rather than on getting accurate estimates of the classical competition parameters model. He proposed a general model formulation in terms of the so-called resource availability functions and proved that the curvature of such a functions determine the curvature of the model nullclines. In contrast to predator–prey models [7,11,12,17,32], most of the other variations of the classical model are phenomenological as in [5,34] (and references citing these papers), but also justifying the form of the species interference term based on ‘food encounters’ [31] on available resources [14] or on a cooperation–competition mechanism [38]. Also in [1,27] an elaborated social model is proposed, in which the individuals of one population gather together in herds, while the other one shows a more individualistic behaviour, so that interactions among the two populations occur mainly through the perimeter of the herd.

The departure assumption in this work is that competing takes time rather than being instantaneous. In other words, two individuals of different species that compete for a given resource do need to invest certain amount of time to get this resource. The model presented herein extends the classical interference competition model [13] (see also [4]) that becomes a particular case when competition is assumed to be instantaneous. The mechanism is essentially that used in Holling works [17,18]. Indeed, the interference term of the model takes the form of a Holling type II term [17] that we call *Holling type II competitive response to interference time*.

As a result, we found a range of parameter values that leads to the same competition outcomes as in the classical model. In addition, we have found also competition outcomes not allowed by the classical model. In the so-called *bi-stable conditional coexistence (in favour of one of the species)* either species coexist or one of them goes extinct, depending on the initial number of individuals (i.e. due to priority effects). There is also the so-called *tri-stable conditional coexistence* scenario that allows either species coexistence or any of them to go extinct due to priority effects.

The manuscript is organized as follow: in Section 2, we derive the above-mentioned model. We also analyze there those scenarios that are the same as in the classical model. In Section 3, we gain an insight on the role of the competitive response by considering

that only individuals of one species expend time in competition. In Section 4, we consider the complete model with competitive response on both species. The system can be analytically analyzed under the assumptions of either symmetric (Section 4.1) or asymmetric (Section 4.2) competition. These results are completed in Section 4.3 with numerical simulations on the most general model. Finally, Section 5 is devoted to the discussion of results and to drawn conclusions.

2. The Holling type II competition model

The departure model is the classical Lotka–Volterra competition model

$$\begin{aligned} x'_1 &= r_1x_1 - a_{11}x_1^2 - a_{12}x_1x_2 \\ x'_2 &= r_2x_2 - a_{22}x_2^2 - a_{21}x_1x_2 \end{aligned} \tag{1}$$

where x_i and $r_i > 0$ stand for the amount of individuals and the intrinsic growth rate of species $i = 1, 2$, respectively. Coefficients $a_{ij} > 0$ account for intra ($i = j$) and inter ($i \neq j$) species competition, for $i, j = 1, 2$.

The key assumption of the classical model (1) is that the *per capita* growth rate of species i decreases linearly with x_i and x_j ($i \neq j$), i.e.

$$\frac{x'_i}{x_i} = r_i - a_{ii}x_i - a_{ij}x_j, \quad i \neq j, \quad i, j = 1, 2$$

In particular, it means that given a fixed number of individuals of species j , the competitive pressure that species $j \neq i$ exerts over species i increases as the number of individuals of species i increases. This assumption may not always make sense on interference competition if competing takes time, since a fixed number of individuals of species j can not interfere the same on species i when competing with, lets say, 10 or 1000 individuals of species i .

We propose an alternative formulation that is an adaptation of [17,18] to the current context. As in [17], we assume that the probability of a *given individual* of species i to encounter an individual of species $j \neq i$ within a fixed time interval T (in a fixed region) depends linearly on the number of individuals of species j . Then, the number N_i of competitors of species $i \neq j$ that become extinct due to the interference of a *single individual* of species $j \neq i$ is given by

$$N_i = aT_{\text{actv}}x_i$$

where x_i is the total amount of individuals of species i , T_{actv} stands for the time that individuals are active (searching for/defending resources or territories, matching, . . .), a is the product of the resources finding rate times the probability of meeting a competitor; thus a is a constant equivalent to Holling’s discovery rate. If interference does not take time, $T = T_{\text{actv}}$; otherwise $T > T_{\text{actv}}$. Let T_{int} be the average time that interference takes, so that $T_{\text{actv}} = T - T_{\text{int}}N_i$, that implies

$$N_i = aT_{\text{actv}}x_i = a(T - T_{\text{int}}N_i)x_i$$

that is equivalent to

$$N_i = \frac{aTx_i}{1 + aT_{\text{int}}x_i} \tag{2}$$

that we call *Holling type II competitive response to interference time*. Plugging this expression in system (1) and relabelling coefficients yields

$$\frac{x'_i}{x_i} = r_i - a_{ii}x_i - \frac{a_{ij}x_j}{1 + a_i x_i}, \quad i \neq j, i, j = 1, 2 \tag{3}$$

Thus, the inter-species competition coefficient is constant only in case of instantaneous interactions (i.e. $a_i = 0$ due to $T_{int} = 0$). Otherwise, the impact of species j on species i is density dependent, a decreasing function of x_i for a fixed amount of individuals of species j .

Note that in general $a_1 \neq a_2$, since the searching rates, the probabilities of finding other species' competitors or the time spent competing/snatching resources can be different for each species due to phenotypical and/or behavioural traits.

Also, in this work we focus on mechanisms that facilitate species coexistence. Thus, even if it could make sense, we do not consider the effect of the time elapsed when competing with conspecifics. Doing so we stress the inter-species dynamics and avoid possible compensatory effects (of the time invest in intra/inter-species competition) that are beyond the scope of this work.

In the sequel, we analyze system (3) and compare the competition outcomes to those yield by the classical competition model (1). Let us first rewrite system (3) in a suitable way by setting $u_i := a_{ii}x_i/r_i$, $c_{ij} := a_{ij}/(r_i a_{ii})$ and $c_i := a_i/a_{ii}$, that yields

$$\begin{aligned} u'_1 &= r_1 \left(u_1 - u_1^2 - \frac{c_{12}u_1u_2}{1 + c_1u_1} \right) \\ u'_2 &= r_2 \left(u_2 - u_2^2 - \frac{c_{21}u_2u_1}{1 + c_2u_2} \right) \end{aligned} \tag{4}$$

Note that the *competitive strength* c_{ij} is the ration of the inter-species and intra-species dynamics rates. Also, c_i is the ratio of the capability of endure competitors (meaning that the larger is c_i , the more time needs a competitor to make species i surrender) and the intra-species competition rates.

For the convenience of the reader, we recall the possible outcomes of the classical competition model, that are summarized in Figure 1:

Theorem 2.1: Consider system (4) with $c_1 = c_2 = 0$. Then, for any solution with initial values in the positive cone

- (1) $E_0^* := (0, 0)$ is globally asymptotically stable if, and only if $r_i < 0$, for $i = 1, 2$.
- (2) $E_1^* := (1, 0)$ is globally asymptotically stable if $0 < c_{12} < 1$ and $c_{21} \geq 1$.
- (3) $E_2^* := (0, 1)$ is globally asymptotically stable if $0 < c_{21} < 1$ and $c_{12} \geq 1$.
- (4) The equilibrium point

$$E_3^* = \left(\frac{1 - c_{12}}{1 - c_{12}c_{21}}, \frac{1 - c_{21}}{1 - c_{12}c_{21}} \right)$$

is globally asymptotically stable if $0 < c_{12} < 1$ and $0 < c_{21} < 1$.

- (5) E_3^* is unstable if $c_{12} > 1$ and $c_{21} > 1$. In such a case, E_1^* and E_2^* are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through E_3^* .

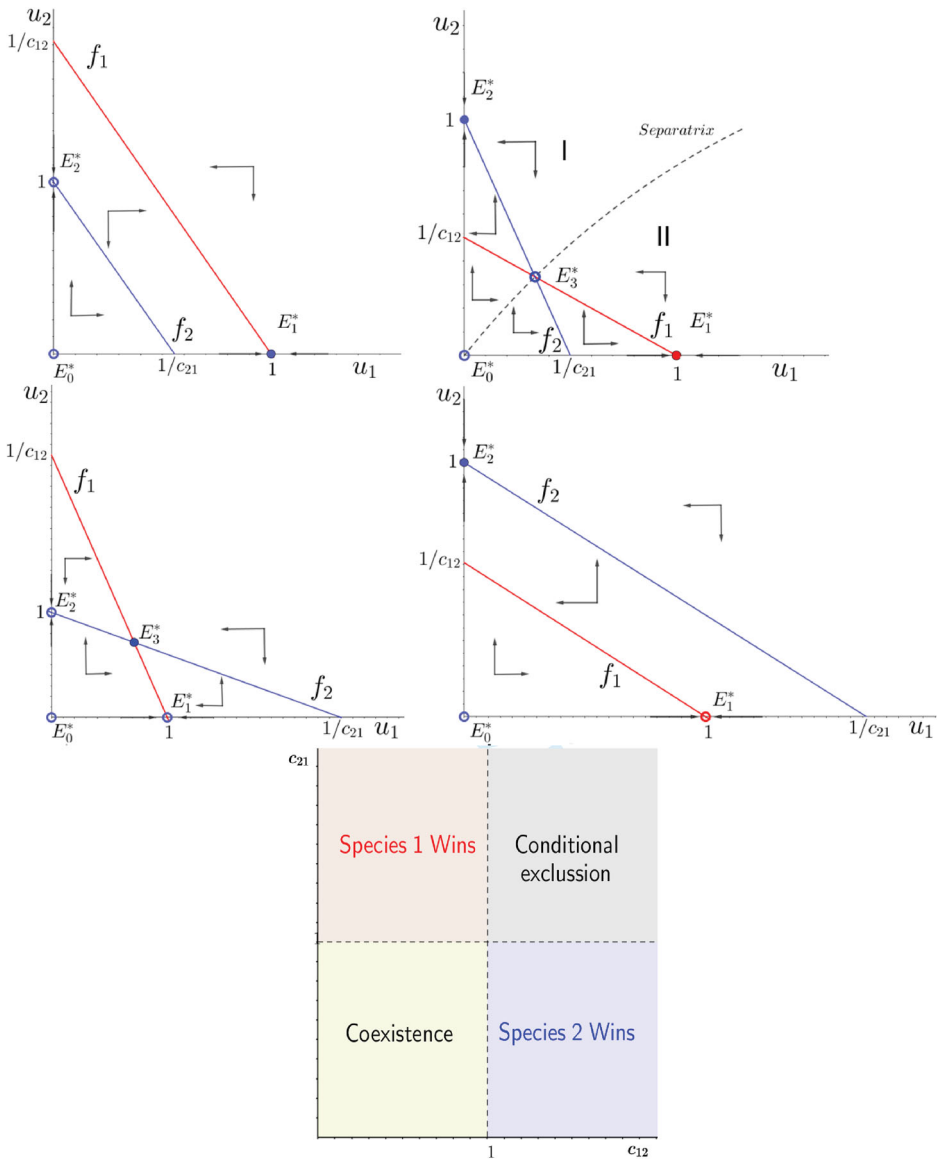


Figure 1. Top panel: possible phase portraits of the classical competition system (system (4)) with $c_1 = c_2 = 0$. Bottom panel: species competition outcomes as function of the competitive strength c_{12} and c_{21} .

Proof: See Section 3.5 in . ■

Conditions in Theorem 2.1 state $c_{ij} = 1, i \neq j$, as a threshold value to compare with the competitive strength $c_{ij}, i \neq j$. In short, species j can not drive species i to extinction if, and only if, the competitive strength $c_{ij}, i \neq j$, of species j on species i is less than 1 (see Figure 1 for a graphical summary).

We next show that system (4) is well behaved, in the sense of the following proposition:

Theorem 2.2: Consider system (4). Then,

- (1) The axes are forward invariant.
- (2) The solutions are bounded from above.
- (3) The positive cone $\mathbb{R}_+^2 = (0, +\infty) \times (0, +\infty)$ is forward invariant.

Proof: Statement 1 follows from the fact that any solution with initial values on one the (say) u_1 axes, fulfills an uncoupled system that consists of the logistic equation $u_1' = r_1 u_1(1 - u_1)$ and $u_2' = 0$. Regarding 2, any solution of equation i is bounded from above by the solutions of the logistic equation $u_i' = r_i u_i(1 - u_i)$, $i = 1, 2$. The third item is consequence of 1 and 2. ■

The following result establishes the existence and stability properties of the so-called trivial and semi-trivial equilibrium points of system (4), that is the same as in the classical model. From now on, we assume that $r_i > 0$ for $i = 1, 2$.

Theorem 2.3: Consider system (4). Then,

- (1) The trivial equilibrium point $E_0^* = (0, 0)$ is unstable (note that $r_i > 0$).
- (2) There exist semi-trivial equilibrium points $E_1^* = (1, 0)$ and $E_2^* = (0, 1)$. Besides:
 - (a) E_i^* is asymptotically stable if $c_{ji} > 1$, $i \neq j$.
 - (b) E_i^* is unstable stable if $c_{ji} < 1$, $i \neq j$.

Proof: The existence of E_i^* , $i = 0, 1, 2$, follows from direct calculations. The stability conditions follow from an standard analysis of the eigenvalues of the Jacobian matrix. ■

The next sections are devoted to understand the effect on the competition outcome of considering a Holling type II competition term in just one species.

3. Holling type II response on just one species

In order to gain an insight on the role of the competitive response, we first assume that only species 2 spends time when competing species 1. Thus, we analyze system

$$\begin{aligned} u_1' &= r_1 \left(u_1 - u_1^2 - \frac{c_{12}u_1u_2}{1 + c_1u_1} \right) \\ u_2' &= r_2(u_2 - u_2^2 - c_{21}u_1u_2) \end{aligned} \tag{5}$$

System (5) is a particular case of system (4), so that we already know that it is well behaved. Proposition 2.3 also holds in relation to the existence and local stability of the trivial and semi-trivial equilibrium points.

In the sequel, we focus on the non-trivial equilibrium points. Note that the nullcline $u_2 = f_2(u_1)$ that solves $u_2' = 0$ is either $u_2 = 0$ or an oblique straight line, as in the classical model. In contrast, the nullcline $u_2 = f_1(u_1)$ that solves $u_1' = 0$ is either $u_1 = 0$ or a parabola. This feature is behind the differences between the outcomes of the classical model and system (5), see Figure 2 and note that panel (v) leads to a dynamical scenario that is not covered by the classical system (see Figure 1).

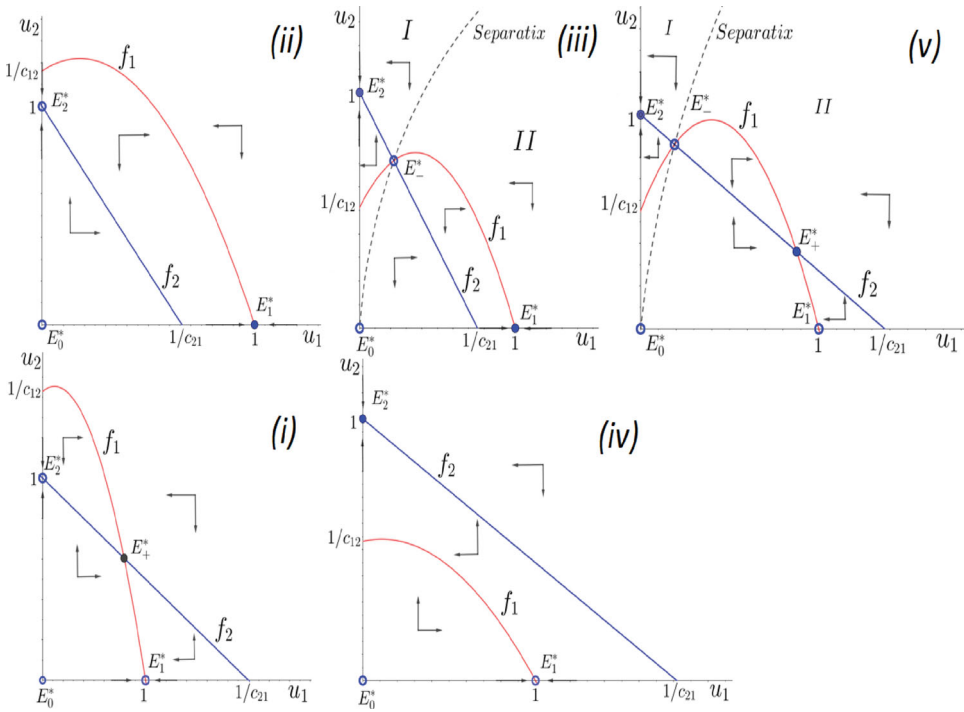


Figure 2. Possible phase portrait of system (5).

Indeed, Figure 2 suggest that most of the outcomes (4 over 5) of system (5) are qualitatively the same as in the classical model. The following result displays conditions that describe those scenarios.

Theorem 3.1: Consider system (5). Then, for any solution with initial values in the positive cone:

- (1) E_1^* is globally asymptotically stable if, and only if, $c_{12} \leq 1$ and $c_{21} \geq 1$.
- (2) E_2^* is globally asymptotically stable if, and only if,

$$(1 - c_1 - c_{12}c_{21})^2 < 4c_1(c_{12} - 1). \tag{6}$$

- (3) Assume now that $c_{12} < 1$ and $c_{21} < 1$. Then, there exists an equilibrium point

$$E_+^* = (u_{1+}^*, u_{2+}^*) \tag{7}$$

where

$$u_{1+}^* = \frac{(c_1 + c_{12}c_{21} - 1) + \sqrt{(c_1 + c_{12}c_{21} - 1)^2 - 4c_1(c_{12} - 1)}}{2c_1},$$

and

$$u_{2+}^* = 1 - c_{21}u_{1+}^*$$

that is globally asymptotically stable to the positive cone.

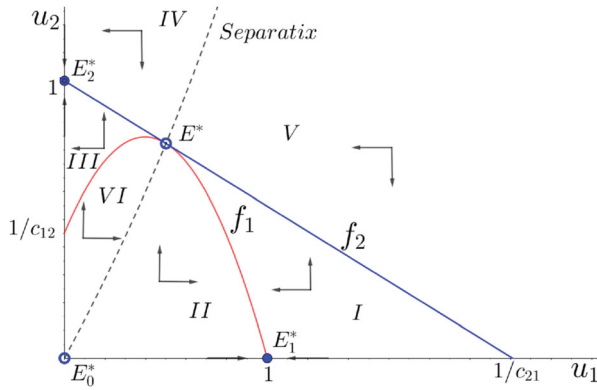


Figure 3. Phase portrait related to tangent nullclines. Solid points denote the locally asymptotically stable equilibrium points E_1^* and E_2^* while the equilibrium E^* is non-stable.

(4) Assume that $c_{12} > 1$ and $c_{21} > 1$. Then there exists an equilibrium point

$$E_-^* = (u_{1-}^*, u_{2-}^*) \tag{8}$$

where

$$u_{1-}^* = \frac{(c_1 + c_{12}c_{21} - 1) - \sqrt{(c_1 + c_{12}c_{21} - 1)^2 - 4c_1(c_{12} - 1)}}{2c_1},$$

and

$$u_{2-}^* = 1 - c_{21}u_{1-}^*$$

that is unstable, while E_1^* and E_2^* are stable, each of which has a basin of attraction defined by a separatrix passing through E_-^* .

Note that conditions in statements (1)–(4) avoid (i) the case of two interior equilibrium points (see Figure 2(v)) and (ii) the case of tangent nullclines in the first quadrant (see Figure 3).

Proof: Consider the nullclines associated to the flow of system (5) defined by

$$f_1(u_1) = (1 - u_1)(1 + c_1u_1)/c_{12}, \quad f_2(u_1) = 1 - u_1c_{21}$$

that is, a parabola and a straight line (see Figure 2) so that the non-trivial equilibrium points are the solutions to the second degree equation resulting from $f_1(u_1) = f_2(u_2)$, that is

$$c_1u_1^2 + (1 - c_1 - c_{12}c_{21})u_1 + c_{12} - 1 = 0 \tag{9}$$

As for statement (1), being E_1^* globally asymptotically stable implies that there is no interior equilibrium points on the positive cone. Thus, either $f_1(u_1) > f_2(u_1)$ for all $u_1 \in [0, 1]$ (that is, $c_{12} \leq 1$ and $c_{21} \geq 1$ and nullclines meet outside the positive cone) or condition (6) holds (that is equivalent to the discriminant of the solution of Equation (9) being negative

and nullclines do not meet). However condition (6) needs $c_{12} > 1$, which implies (by linearization) that E_1^* is unstable that is a contradiction with the departure hypothesis, so that $c_{12} \leq 1$ and $c_{21} \geq 1$ holds. Conversely, assume that $c_{12} \leq 1$ and $c_{21} \geq 1$. Then, analyzing the phase portrait as in [4] yields the global stability of E_1^* .

Regarding statement 2, we have already said that condition (6) is equivalent to the discriminant of the solution of Equation (9) being negative. That is to say that f_1 and f_2 do not meet anywhere which, given the geometry of the nullclines, yields the global stability of E_2^* .

The remaining statements follow *mutatis mutandi* the proof of the corresponding results for classical competition model; see, for instance, [4] or . ■

We turn our attention to these settings that lead to new dynamical scenarios with respect to those displayed by the classical system. It will turn out that the following curve, that results from equating to zero the discriminant of the solution of Equation (9) and solving the resulting equation on c_{21} , plays a key role.

Lemma 3.2: *Consider the function*

$$\psi_{c_1}(c_{12}) := \frac{1 - c_1 + 2\sqrt{c_1(c_{12} - 1)}}{c_{12}}, \quad c_{12} \geq 1 \tag{10}$$

then, ψ_{c_1} is an unimodal function such that

- (1) $\psi_{c_1}(1) = 1 - c_1$ and $\lim_{c_{12} \rightarrow +\infty} \psi_{c_1}(c_{12}) = 0$.
- (2) For $c_1 > 1$, $\psi_{c_1}(c_{12}) = 0$ at $c_{12} = 1 + \frac{(c_1-1)^2}{4c_1}$.
- (3) The maximum is reached at $c_{12} = c_1 + 1$ and $\psi_{c_1}(c_1 + 1) = 1$.

Proof: It follows from direct calculations. ■

In the following result, we assume that $c_{12} > 1$ and $c_{21} < 1$, so that in the classical model species 2 wins regardless of the initial number of individuals of each species. Then, if the species 1 competitive ability is not too small so that $1 > c_{21} > \psi_{c_1}(c_{12})$, then species may either coexist or species 2 win unconditionally, depending on initial values, what we call *bi-stable conditional coexistence in favour of species 1*. Otherwise, species 2 wins always.

Theorem 3.3: *Consider system (5) and assume that $c_{12} > 1$ and $c_{21} < 1$. Then, for any solution with initial values in the positive cone:*

- (1) *The condition $c_{21} < \psi_{c_1}(c_{12})$ implies that the semi-trivial equilibrium point E_2^* is globally asymptotically stable.*
- (2) *Assume now that $c_{21} = \psi_{c_1}(c_{12})$. Then*

$$\hat{E}^* := (u_1^*, u_2^*) = \left(\frac{c_1 + c_{12}c_{21} - 1}{2c_1}, 1 - \frac{c_1 + c_{12}c_{21} - 1}{2c_1}c_{21} \right)$$

is the unique equilibrium point of system (5) in the positive cone if, and only if,

$$0 < \frac{c_1 + c_{12}c_{21} - 1}{2c_1} < 1 \tag{11}$$

In this case E_1^* is unstable, and there exists a separatrix passing through E^* that divides the positive cone into two open regions R_1 and R_2 such that $E_i^* \in \partial R_i$, $i = 1, 2$ (where ∂R_i stands for the boundary of R_i) such that any solution with initial values in R_1 converges to E_* while any solution with initial values in R_2 converges to E_2^* .

- (3) Assume now that $c_{21} > \psi_{c_1}(c_{12})$ and $1 < c_{12} < c_1 + 1$. Then there exist two equilibrium points in the positive cone if, and only if, condition (11) holds. In such a case, the equilibrium point E_-^* (defined in (8)) is unstable while E_2^* and E_+^* (defined in (7)) are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through E_-^* .
- (4) Assume now that $1 > c_{21} > \psi_{c_1}(c_{12})$ and $c_{12} > c_1 + 1$. Then the semi-trivial E_2^* is asymptotically stable.
- (5) If condition $0 < (1 + c_1 - c_{12}c_{21})/2c_1 < 1$ fails, no positive equilibrium exists.

Proof: Let us recall that the non-trivial equilibrium points $E_{\pm}^* = (u_{1\pm}^*, u_{2\pm}^*)$ are the solutions to Equation (9) and that

$$u_{1\pm}^* = \frac{c_1 + c_{12}c_{21} - 1 \pm \sqrt{(c_1 + c_{12}c_{21} - 1)^2 - 4c_1(c_{12} - 1)}}{2c_1}$$

Equating to zero the discriminant of the above expression and solving the resulting equation on c_{21} yields $c_{21} = \psi_{c_1}(c_{12})$ as defined in (10).

- (1) Condition $c_{21} < \psi_{c_1}(c_{12})$ with $1 < c_{12} < \infty$ is equivalent to Equation (9) to have complex roots, so that there are no non-trivial equilibrium points. Analyzing the flow of the phase portrait as in [4] yields 1.
- (2) The discriminant in $u_{1\pm}^*$ is equal zero when $c_{21} = \psi_{c_1}(c_{12})$. Therefore, E_+^* and E_-^* collide into \hat{E}^* , that is in the positive cone.

Regarding the stability, we claim that this is a degenerate case, in the sense that zero is an eigenvalue of the Jacobian matrix of the flow of system (5) at E^* . Namely, consider the Jacobian matrix of system (5) at any $(u_1, u_2) \in \mathbb{R}^2$

$$J(u_1, u_2) = \begin{pmatrix} r_1 - 2r_1u_1 - r_1 \frac{c_{12}u_2}{(1 + c_1u_1)^2} & -r_1 \frac{c_{12}u_2}{1 + c_1u_1} \\ -r_2c_{21}u_2 & r_2(1 - 2u_2 - c_{21}u_1) \end{pmatrix} \tag{12}$$

At an equilibrium point (u_1^*, u_2^*) of system (5) it holds that

$$1 - u_1^* - \frac{c_{12}u_2^*}{1 + c_1u_1^*} = 0 \quad 1 - u_2^* - c_{21}u_1^* = 0$$

thus, the Jacobian matrix (12) at the equilibrium point (u_1^*, u_2^*) becomes

$$J(u_1^*, u_2^*) = \begin{pmatrix} r_1 - 2r_1u_1^* - r_1 \frac{1 - u_1^*}{1 + c_1u_1^*} & -r_1 \frac{c_{12}u_2^*}{1 + c_1u_1^*} \\ -r_2c_{21}u_2^* & -r_2u_2^* \end{pmatrix} \tag{13}$$

Zero is an eigenvalue of matrix (13) if, and only if, $|J(u_1^*, u_2^*)| = 0$. Direct calculation lead to

$$|J(u_1^*, u_2^*)| = \frac{-r_1r_2u_1^*u_2^*}{1 + c_1u_1^*} [c_1 - 1 - 2c_1u_1^* + c_{12}c_{21}]$$

so that

$$|J(u_1^*, u_2^*)| = 0 \Leftrightarrow u_1^* = \frac{c_1 + c_{12}c_{21} - 1}{2c_1}$$

that is, at \hat{E}^* .

Besides, consider the corresponding phase portrait (see Figure 3). A first claim is that regions I and III are trapping regions, meaning that any solution entering one of them cannot leave such a region. It has two consequences: on the one hand, it precludes the existence of limit cycles.

On the other hand, solutions with initial values in region I converge to E_1 while solutions with initial values in region III converge to E_2^* (Figure 3).

- (3) We already know that condition $c_{21} > \psi_{c_1}(c_{12})$ ensures that there exist two real non-trivial (nor semi-trivial) equilibrium points E_{\pm}^* . In addition, E_{\pm}^* are in the positive cone if, and only if, $0 < u_{1\pm}^* < 1$, since $f_1(u_1) < 0$ for $u_1 > 1$.

Note that $c_{21} > \psi_{c_1}(c_{12})$, $c_{12} > 1$ along with condition (11) imply that $0 < u_{1\pm}^*$. Besides, $u_{1+}^* < 1$ is equivalent to

$$\sqrt{(c_1 + c_{12}c_{21} - 1)^2 - 4c_1(c_{12} - 1)} < c_1 + 1 - c_{12}c_{21} \tag{14}$$

The right-hand side of the previous inequality is positive since $1 < c_{12} < 1 + c_1$ and $0 < c_{21} < 1$. Then squaring both sides of (14) and rearranging terms we get that (14) is equivalent to

$$c_{21} - 1 < 0$$

that holds because $0 < c_{21} < 1$. As for the stability, consider the particular case that $c_{12} = c_{21} = 1$. Thus, $E_-^* = E_2^*$ while $E_+^* = E_1^*$. Let us argue on $E_+^* = E_1^*$. In this case, direct calculations show that E_+^* is hyperbolic and asymptotically stable, in particular,

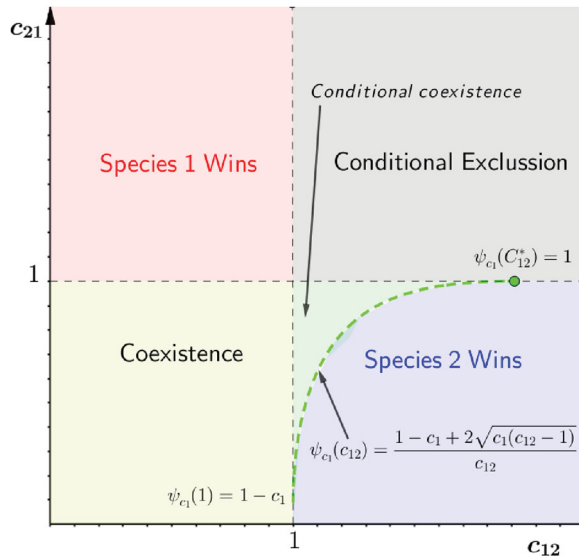


Figure 4. Competition outcomes of system (5) as function of the competitive strengths c_{12}, c_{21} .

its eigenvalues are simple and negative, so that this feature remains the same under small perturbations on $c_{12} \gtrsim 1$ and $c_{21} \lesssim 1$. Reasoning in the same way we get that E_-^* is a saddle for small perturbations on $c_{12} \gtrsim 1$ and $c_{21} \lesssim 1$. We shall prove that the sign of the eigenvalues remain constant under the assumptions of 2(a). Given the continuity of the spectrum, we need to prove that zero is not an eigenvalue of the Jacobian matrix neither at E_+^* nor E_-^* . But we already know from the previous statement that it happens when $E_+^* = E^* = E_-^*$.

- (4) Note that $f_1(0) = 1/c_{12}, f_2(0) = 1$ and $f_1(1) = 0, f_2(0) = 1 - c_{21}$. Thus, $f_2(0) > f_1(0)$ and $f_2(1) > f_1(1)$, so that no positive equilibrium points exist.
- (5) It follows from the previous discussion. ■

So we have completed the analysis of system (5). Figure 4 summarizes the possible outcomes of system (5), that extends those allowed by the classical system (1) (see the bottom panel of Figure 1). The above results are deeply discussed in Section 5.

4. Holling type II response on both species

We turn now our attention to the complete model (4). Section 3 suggests that we must expect either settings such that the classic competition model and system (4) behave qualitatively the same (and differences are, if any, in the transient time) or such that dynamics is a little bit more complicated and expands the coexistence conditions.

After Proposition 3.1, we focus on the existence and stability of the non-trivial equilibrium points. The nullclines of system (4) are parabolas, defined by

$$\begin{aligned} u_2 = f_1(u_1) &= (1 - u_1)(1 + c_1 u_1)/c_{12}, \\ u_1 = f_2(u_2) &= (1 - u_2)(1 + c_2 u_2)/c_{21} \end{aligned} \tag{15}$$

so that the equilibrium points are given by the solutions to the fourth degree equation

$$P(u_1) = \gamma_4 u_1^4 + \gamma_3 u_1^3 + \gamma_2 u_1^2 + \gamma_1 u_1 + \gamma_0 = 0 \tag{16}$$

where

$$\begin{aligned} \gamma_4 &= -c_1^2 c_2 \\ \gamma_3 &= 2c_1 c_2 (c_1 - 1) \\ \gamma_2 &= 2c_1 c_2 - c_1 (c_2 - 1) c_{12} - c_2 (c_1 - 1)^2 \\ \gamma_1 &= (c_1 - 1)(c_2 - 1) c_{12} - 2(c_1 - 1) c_2 - c_{12}^2 c_{21} \\ \gamma_0 &= (c_2 + c_{12})(c_{12} - 1) \end{aligned} \tag{17}$$

It is well known that there exists a closed formula to solve this equations but, unfortunately, its expression is too involved to get any biological insight. Then, we adopt a numerical approach to analyze system (4). However, there are two ecologically meaningful scenarios, symmetric and asymmetric competition [39], that lead to simplifications in (17) that allow an analytic study that we address next.

4.1. Symmetric competition and Holling type II competitive response

Symmetric competition takes place, for instance, between individuals of different species with similar phenotypic traits [39]. This idea can be translated to system (4) by setting the model coefficients as

$$c_1 = c_2 \equiv c, \quad c_{12} = c_{21} \equiv \hat{c} \tag{18}$$

see [22]. In such a case, coefficients (17) specialize into

$$\begin{aligned} \gamma_4 &= -c^3 \\ \gamma_3 &= 2c^2(c - 1) \\ \gamma_2 &= 2c^2 - c(c - 1)\hat{c} - c(c - 1)^2 \\ \gamma_1 &= \hat{c}(c - 1)^2 - 2(c - 1)c - \hat{c}^3 \\ \gamma_0 &= (c + \hat{c})(\hat{c} - 1) \end{aligned} \tag{19}$$

It turns out that $c = 1$ and $\hat{c} = 1$ are candidate to be threshold values for the behaviour of the model (for instance, think of Descartes’ Rule). We first claim that the nullclines are symmetric with respect to the $u_1 = u_2$ line, namely

Lemma 4.1: *Consider the nullcline curves (15) with coefficients (18), so that*

$$\begin{aligned} f_1(u_1) &= -\frac{c}{\hat{c}} \left[u_1 - \frac{c - 1}{2c} \right]^2 + \frac{(c + 1)^2}{4c\hat{c}} \\ f_2^{-1}(u_1) &= \frac{c - 1 \pm \sqrt{(c + 1)^2 - 4c\hat{c}u_1}}{2c} \end{aligned}$$

are symmetrical with respect to the straight line $u_2 = u_1$, meaning that they are reciprocal functions

- (a) $f_2(f_1) = u_1, \forall u_1 \in [(c - 1)/2c, \infty)$.
- (b) $f_1(f_2) = u_1, \forall u_1 \in (-\infty, (c + 1)^2/4c\hat{c}]$.

*As a consequence, there exists two equilibrium points $E_{\pm}^{**} := (u_{1\pm}^{**}, u_{1\pm}^{**})$ on the $u_1 = u_2$ line with coordinates*

$$u_{1\pm}^{**} = \frac{c - \hat{c} - 1 \pm \sqrt{(c - \hat{c} - 1)^2 + 4c}}{2c} \tag{20}$$

*where E_{+}^{**} is in the positive cone while E_{-}^{**} is in the third quadrant.*

Proof: It follows from direct calculations. ■

The following proposition describes the dynamics of the model under symmetric competition and includes a *tri-stability conditional coexistence* scenario that is not allowed by the classical model (see Figure 5).

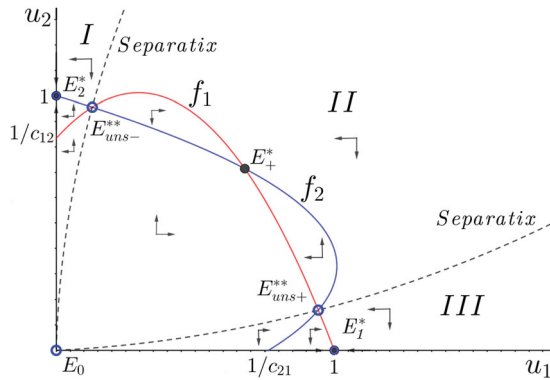


Figure 5. Phase portrait in the symmetric competition scenario that displays the tri-stability conditional coexistence outcome.

Theorem 4.2: Consider system (4) along with the symmetry conditions $c_1 = c_2 \equiv c$ and $c_{12} = c_{21} \equiv \hat{c}$. Then

- (1) For any $0 < \hat{c} < 1$, the equilibrium point E_+^{**} defined by (20) is a global attractor to the positive cone. Note that E_+^{**} is on the line $u_2 = u_1$.
- (2) Assume now that $\hat{c} > 1$, so that the semi-trivial equilibrium points E_1^* and E_2^* are locally asymptotically stable, and consider $c_+^* := \hat{c} - 1 + 2\sqrt{\hat{c}(\hat{c} - 1)}$. Then,
 - (a) For any $c \in (0, c_+^*]$, E_+^{**} is a saddle, so that there exists a separatrix passing through E_+^{**} that defines the basins of attraction of E_1^* and E_2^* .
 - (b) For any $c > c_+^*$ E_+^{**} is locally asymptotically stable. Besides, there is a bifurcation as c crosses the threshold value $c = c_+^*$. Namely, two additional unstable equilibrium points

$$E_{\text{uns}\pm}^{**} = (u_{1\text{uns}\pm}^{**}, u_{2\text{uns}\pm}^{**})$$

emerge from E_+^* , one below the line $u_2 = u_1$ and the other one above such a line, where

$$u_{1\text{uns}\pm}^{**} = \frac{c + \hat{c} - 1 \pm \sqrt{(c + \hat{c} - 1)^2 - 4(\hat{c}^2 + (c - 1)\hat{c} - c)}}{2c} \tag{21}$$

Furthermore, there exist two separatrices, each of them passing through $E_{\text{uns}\pm}^{**}$ that defines the basins of attraction of E_1^* , E_2^* and E_+^{**} , respectively.

Proof: Let us recall that system (4) possesses, at most, four equilibrium points and lemma 4.1 yields the expression of two of them.

- (1) We will show that $0 < \hat{c} < 1$ implies the existence of two equilibrium points located at the second and fourth quadrant, respectively. Indeed, $0 < \hat{c} < 1$ is equivalent to $1/\hat{c} > 1$ so that considering the nullclines defined in (15), it follows that $\lim_{u_1 \rightarrow -\infty} f_1(u_1) = -\infty$ and $\lim_{u_2 \rightarrow -\infty} f_2(u_2) = -\infty$, that is, $f_1(u_1)$ and $f_2(u_2)$ meet somewhere in the second quadrant. The symmetry of the nullclines imply that there exists another equilibrium point in the fourth quadrant. The semi-trivial equilibrium points E_1^* and E_2^*

are unstable, since $0 < \hat{c} < 1$. There exist two trapping regions in the phase portrait defined by the nullclines and the axes, with vertexes $\{(0, 1), (0, 1/\hat{c}), E_+^{**}, \}$ and $\{(1, 0), (1/\hat{c}, 0), E_+^{**}, \}$ that preclude the existence of limit cycles. Therefore, all the orbits converge to E_+^{**} , since all the solutions are bounded, as stated in Proposition 2.2. The case $\hat{c} = 1$ follows from the previous discussion.

- (2) Dividing $P(u_1)$, the polynomial (16) with coefficients (19), by $(u_1 - u_{1-}^{**})(u_1 - u_{1+}^{**})$ yields the second degree polynomial

$$c^2 u_1^2 + c(1 - c - \hat{c})u_1 + \hat{c}^2 + (c - 1)\hat{c} - c$$

whose roots are the u_1 component of the other two equilibrium points, namely (21). Therefore, whether $u_{1\text{uns}\pm}^{**}$ is real or complex depends on the discriminant of the right-hand side of Equation (21). Equating to zero the discriminant of (21) is equivalent to

$$c = c_{\pm}^* := \hat{c} - 1 \pm 2\sqrt{\hat{c}(\hat{c} - 1)}$$

where $c_-^* < 0$ and $c_+^* > 0$. Then

- (a) For any $0 < c < c_+^*$ it follows that $u_{\text{uns}\pm}^{**} \in \mathbb{C}$. The stability can be derived as in the proof of 1. Note that the symmetry in the phase portrait implies that the straight $u_1 = u_2$ is invariant by the flow of system (4) and, in fact, it is a separatrix for the basins of attraction of the semi-trivial equilibrium points. Indeed, the orientation of the orbits on $u_1 = u_2$ imply that one of the eigenvalues of the Jacobian at E_+^* is always negative. The orientation of the orbits on the trapping regions with vertexes $\{(0, 1), (0, 1/\hat{c}), E_1^*\}$ and $\{(1, 0), (1/\hat{c}, 0), E_2^*\}$ yield that the other eigenvalue is positive, so that E_+^{**} is a saddle and therefore its fixed point index $i(E_+^{**}) = -1$ (see [19]).
- (b) Direct calculations show that $u_{1+}^* = u_{1+}^{**} = u_{1-}^{**}$ at $c = c_+^*$. Thus, two branches of equilibrium points $E_{\text{uns}+}^{**}$ and $E_{\text{uns}-}^{**}$ bifurcate from E_+^{**} as c crosses the threshold value c_+^* ; in particular, $0 < u_{1-}^{**} < u_{1+}^* < u_{1+}^{**} < 1$ for any $c > c_+^*$ since the square with vertexes $\{(0, 0), (0, 1), (1, 1), (1, 0)\}$ is forward invariant, so that there are no equilibrium points outside such square. The invariance of the fixed point index by homotopy [19] implies that

$$i(E_+^*) + i(E_+^{**}) + i(E_-^{**}) = -1$$

and the geometry (and symmetry) of the phase portrait yields that

$$i(E_+^*) = 1, \quad i(E_+^{**}) = i(E_-^{**}) = -1, \quad c > c_+^*,$$

that means that E_+^* is locally asymptotically stable and E_{\pm}^{**} are saddle points. ■

4.2. Asymmetric competition and Holling type II competitive response

Asymmetric competition [20] takes place, for instance, between individuals of different species with dissimilar phenotypic traits [39]. We impose the following constraints to the model coefficients $c_2 = 1/c_1$, $c_1 = c$ and $c_{21} = 1/c_{12}$, $c_{12} = \hat{c}$, in order to set full

asymmetric competition. Thus, coefficients (17) become

$$\begin{aligned}
 \gamma_4 &= -c \\
 \gamma_3 &= 2(c - 1) \\
 \gamma_2 &= 2 - (1 - c)\hat{c} - (c - 1)^2/c \\
 \gamma_1 &= \hat{c} - (c - 1)(1/c - 1)\hat{c} - 2(c - 1)/c \\
 \gamma_0 &= (1/c + \hat{c})(\hat{c} - 1)
 \end{aligned}
 \tag{22}$$

As before, $c = 1$ and $\hat{c} = 1$ are candidates to be a threshold value for the qualitative behaviour of the solutions of system (4).

We do not perform a complete analysis of the resulting model; we just state conditions that lead to bi-stable conditional coexistence scenarios:

Theorem 4.3: *Consider system (4) along with the asymmetry conditions $c_2 = 1/c_1$ and $c_{12} = 1/c_{21} \equiv \hat{c}$. Then*

- (1) *For any $0 < \hat{c} < 1$, it follows that E_1^* is locally asymptotically stable. Furthermore, there exists $c^{**} > 0$ such that*
 - (a) *For any $0 < c < c^{**}$, there exist two positive equilibrium points E_s^{**}, E_u^{**} such that E_s^{**} and E_1^* are locally asymptotically stable while E_u^{**} is unstable. There is a separatrix passing through E_u^{**} that defines the basins of attraction of E_1^* and E_s^{**} , respectively.*
 - (b) *For any $c > c^{**}$ E_1^* is globally asymptotically stable to the positive cone.*
- (2) *Assume now that $\hat{c} > 1$. Then, E_2^* is locally asymptotically stable and there exists $c^{**} > 0$ such that*
 - (a) *For any $0 < c < c^{**}$ E_2^* is globally asymptotically stable to the positive cone.*
 - (b) *For any $0 < c < c^{**}$ there exist two positive equilibrium points E_s^{**}, E_u^{**} such that E_s^{**} and E_2^* are locally asymptotically stable while E_u^{**} is unstable. There is a separatrix passing through E_u^{**} that defines the basins of attraction of E_2^* and E_s^{**} , respectively.*

Proof: It follows arguing as in Propositions 2.2 and 4.2. ■

4.3. The general case: numerical analysis

As we have already said, the equilibrium points of system (4) are the roots of the 4th degree polynomial Equation (16). These solutions depend on the coefficients (17) that depend on c_i and c_{ij} , that is, on four parameters. Close expressions exist for the roots of (16), but are so involved that we could not derive any biological information from them. We have also attempted to use Cardano’s and Ferrari’s theorem or Sturm’s sequence, Descartes’s rule and Burdan–Fourier theorem with no positive results.

Therefore, we perform a numerical analysis using an algorithm written in MatLab software. From the results found in Sections 3, 4.1 and 4.2 we decided to plot diagrams that display, for fixed values of $c_i, i = 1, 2$, the number of equilibrium points and its stability for c_{12}, c_{ji} ranging in a given interval, as in Figure 7.

As there are no analytical results for the complete model different from those already obtained at the beginning of Section 2, we left the results of the numerical experiments to the discussion and conclusions Section 5.

5. Discussion and conclusions

In this manuscript, we revisit the classical competition model (1) under the assumption that interfering with competitors of other species takes time. We have found that (i) the classical competition model is a particular case of the model derived herein when interactions do not consume time, (ii) the more time interfering with competitions takes the more likely coexistence is and, indeed, (iii) the new model allows multi-stability scenarios.

Geometrically, accounting for the time spent competing bends nullclines from the straight lines found in the classical model into a parabolic shape. This feature has been previously found in [30,38] under different departure hypotheses and not fully analyzed (only qualitatively). Compare the nullcline of species 1 in the classical competition model ($u_2 = \hat{f}_1(u_1)$, left panel in Figure 6) and in system (4) ($u_2 = f_1(u_1)$, central and right panels in Figure 6), where

$$u_2 = \hat{f}_1(u_1) := \frac{1}{c_{12}} (1 - u_1) \quad u_2 = f_1(u_1) := \frac{1}{c_{12}} (-c_1 u_1^2 + (c_1 - 1)u_1 + 1) \quad (23)$$

Let us recall that the bounded region defined by the axes and the nullcline of species 1 defines the values of the population size of species 2 that allow species 1 to keep growing.

The classical model states that the larger is u_1 , the less tolerant is to the presence of u_2 , meaning that as u_1 increases, u_1 keeps growing only if u_2 decreases (according to the nullcline slope).

On the contrary, accounting for the time spent competing weakens or even reverses this trend, since the region below the nullcline increases with $c_1 > 0$. In words, the more time species 2 needs to snatch resources to species 1, the less time has species 2 to compete with other individuals of species 1. We may say that such a time is moderate for $0 < c_1 < 1$ and large if $1 < c_1$. Looking closer to the nullcline of u_1 in system (4), note that it achieves its maximum $\tilde{u}_2 := (c_1 + 1)^2/(4c_1)$ at $\tilde{u}_1 := (c_1 - 1)/(2c_1)$. Then,

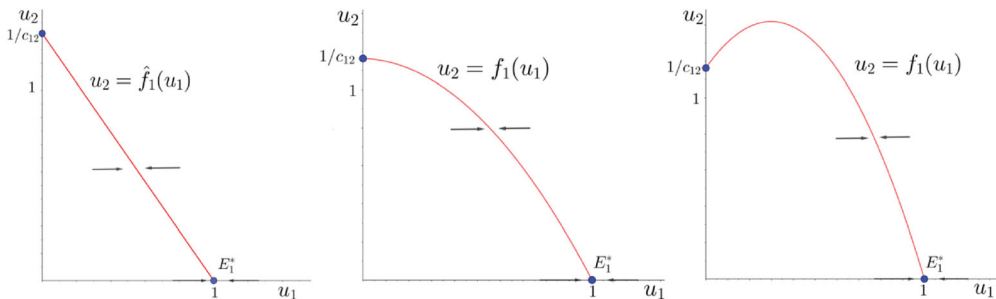


Figure 6. The nullcline $u_1' = 0$ of system (4) for increasing values of c_1 : left, $c_1 = 0$ (i.e. the classical Lotka–Volterra model (1)), centre, $c_1 \in (0, 1)$ and right, $c_1 > 1$.

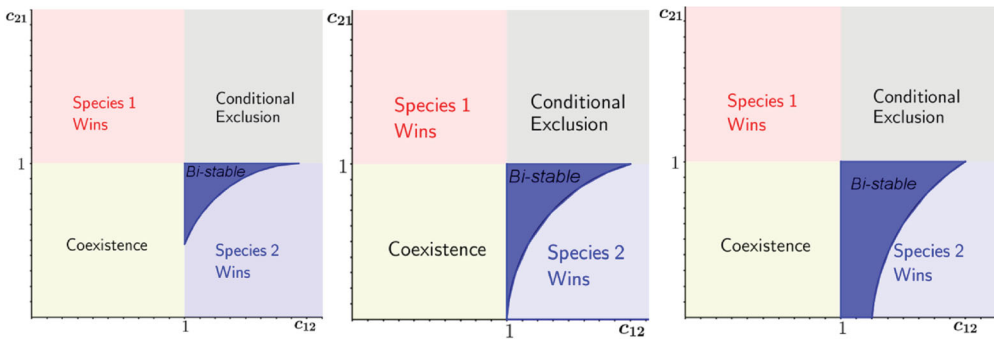


Figure 7. Competition outcomes of system (5) as function of the competitive strengths c_{12} , c_{21} for increasing values of c_1 (from left to right). The code colour is the same as in Figure 1 except the dark blue region that represents bi-stable conditional coexistence region in favour of species 1. The boundary between the blue regions is the graph of $c_{21} = \psi_{c_1}(c_{12})$. The figure is based on numerical calculations (the source code is available in [9]) alingment!!! and has been edited to improve it. Parameter values are $0 < c_{12}$, $c_{21} < 2$, $c_2 = 0$ and, from left to right, $c_1 = 0.3, 1, 1.8$.

- Condition $0 < c_1 < 1$ implies that $\tilde{u}_1 < 0$ and the nullcline defined by f_1 in (23) is decreasing for $u_1 \geq 0$ (see central panel in Figure 6). The behaviour is qualitatively the same as in the classical Lotka–Volterra model, although the effect of the time spent competing is not completely negligible and ‘bends’ the nullcline softening the effect of the other species’ competitive pressure.
- If $c_1 > 1$, geometrically, the maximum of the parabola defined by f_1 in Equation (15) is in the first quadrant (right panel in Figure 6). As a consequence, if $0 < u_1 < \tilde{u}_1$ species 1 keeps growing even if u_2 increases moderately (but reaming below the nullcline). It is possible because there are not so many encounters and, if so, species 2 spends many time competing and can not go immediately for another resource. However, as species 1 growths and crosses the threshold value \hat{u}_1 this trend is reversed, although things are still better for them that in the classical model.

Then, \tilde{u}_1 is a threshold value for u_1 to tolerate an increasing amount of individuals of species 2. Interestingly, note that \tilde{u}_1 is bounded from above while \tilde{u}_2 is unbounded for increasing values of c_1 . On the one hand, that is to say that intra-species competitive pressure will show up at \tilde{u}_1 , since the maximum is reached at $u_1 = \tilde{u}_1$ regardless of $c_1 > 1$. However, if $0 < c_1 < 1$ (so that $\tilde{u}_1 < 0$) intra-species pressure is added to inter-species pressure, although the later is slightly weakened by the little time spent competing. On the other hand, \tilde{u}_2 still increases if c_1 does so. Thus, we can somehow discriminate the tolerance to intra and inter-species crowd. This feature is particularly important to species 1, for instance, when $c_{12} > 1$ and $c_{21} < 1$. In such a case, species 1 will go extinct for small enough values of c_1 , since the nullcline of species 1 is below the nullcline of species 2 (as, for instance, in the bottom right panel in Figure 2). However, for large enough values of c_1 the nullclines switch their position giving rise to a bi-stable conditional coexistence in favour of species 2 scenario (as in the top right panel in Figure 2).

According to [33,38] the common interpretation of the early theory of competition [13,23,35] is that coexistence results when intra-species competition limits species’ density

more strongly than inter-species competition. From this point of view, accounting for the time spent competing balances the estimates of the relative strength of intra and inter-species competition.

Coefficient c_1 is a conglomerate of different factors that include the amount of time spent interfering with the other species T_{int} , the searching rate and the probability of interfering with other species individual. Therefore, it suggests different strategies that may improve species 1 chances to survive. For instance, from a behavioural point of view, the above discussion suggests that resist to species 2 may be beneficial to species 1 [26,28] (note that our model does not take into account possible injuries or harms derived from facing species 2).

Ultimately, the time spent competing becomes a trade off between the competitive abilities of the competing species. We have found a full description of this compensatory mechanism when only one species displays competitive response.

We have already said that species 1 better tolerates competing with species 2 if competition is not instantaneous to species 2. In such a case the curve $c_{21} = \psi_{c_1}(c_{12})$ defined in (10) (see Lemma 3.2) plays a key role.

Let us assume that $0 < c_{21} < 1$ and $1 < c_{12}$, that corresponds to the (unconditional) species 1 exclusion in the classical model. Proposition 3.3 tells us that both species can coexist via bi-stable conditional coexistence if

$$0 < \psi_{c_1}(c_{12}) < c_{21} < 1$$

In words, a larger competitive strength of species 2 can be compensated by a larger ratio of individuals of species 1 if competition takes enough time to species 2. The limits of this trade off are defined by ψ_{c_1} (see Figure 7), that depends on c_1 .

On the contrary (that is, if $c_{21} < \psi_{c_1}(c_{12})$ but still $0 < c_{21} < 1$ and $1 < c_{12}$), species 1 will go extinct regardless of the initial amount of individuals of each species. In such a case, species 2 does not spend time enough to compensate the difference on competitive abilities.

Interestingly, the Holling type II competitive response has no effect on the long term behaviour of the model in case of strong competition ($1 < c_{21}$ and $1 < c_{12}$) and the new region in the $c_{12}c_{21}$ space parameter comprised between $c_{12} = 1$, $c_{21} = 1$ and $c_{21} = \psi_{c_1}(c_{12})$ is, indeed, a kind of transition region between the coexistence region ($0 < c_{21} < 1$ $0 < c_{12} < 1$), the species 1 exclusion region ($1 > c_{21}$ and $1 < c_{12}$) and the conditional exclusion region ($1 < c_{21}$ and $1 < c_{12}$).

Competitive response on both species. In the overall, if competing takes time to both competing species then the competitive pressure is softer, which is beneficial for coexistence.

We have first analyzed the symmetric and asymmetric competition scenarios, that have its own applied interest and for which we have achieved analytical results with close expressions for equilibrium and threshold values.

Assume now that competition is (perfectly) symmetric in the sense of $c_{12} = c_{21} = \hat{c}$ and $c_1 = c_2 = c$. Then, there exists a global positive attractor to the positive cone if $\hat{c} < 1$ and regardless of the value of c . On the other hand, $\hat{c} > 1$ implies that (unconditional) global coexistence is not possible anymore, and either tri-stable conditional coexistence or conditional exclusion will happen, see Figure 8.

The classical model yields one species exclusion due to priority effects but, instead, a new dynamical scenario raises in the form of tri-stable conditional coexistence: depending

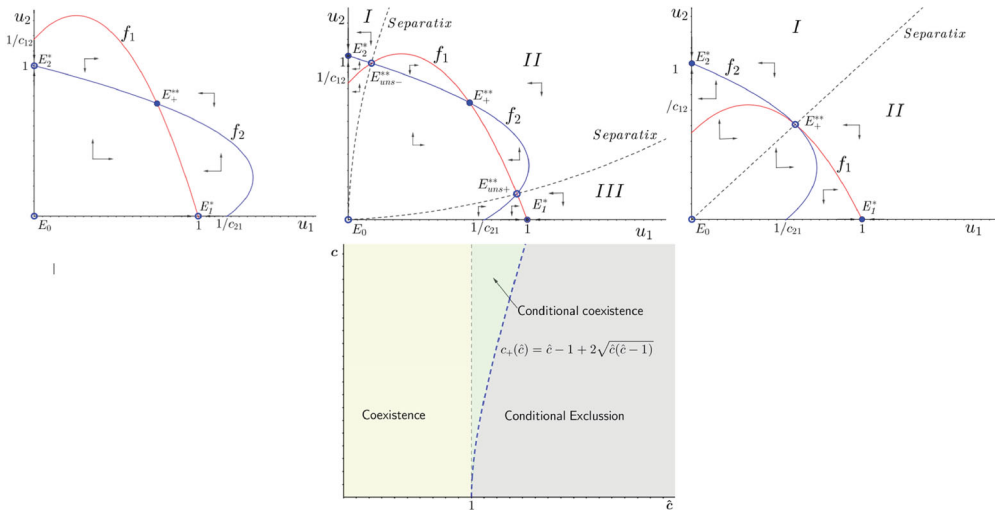


Figure 8. Competition outcomes of system (4) in case of symmetric competition: $c_{12} = c_{21} = \hat{c}$ and $c_1 = c_2 = c$. Top left panel corresponds to global coexistence ($0 < \hat{c} < 1$ and any $c > 0$). Central top panel corresponds to conditional coexistence ($\hat{c} > 1$ and $c > \hat{c} - 1 + 2\sqrt{\hat{c}(\hat{c} - 1)}$). Top right panel corresponds conditional exclusion ($\hat{c} > 1$ and $0 < c < \hat{c} - 1 + 2\sqrt{\hat{c}(\hat{c} - 1)}$).

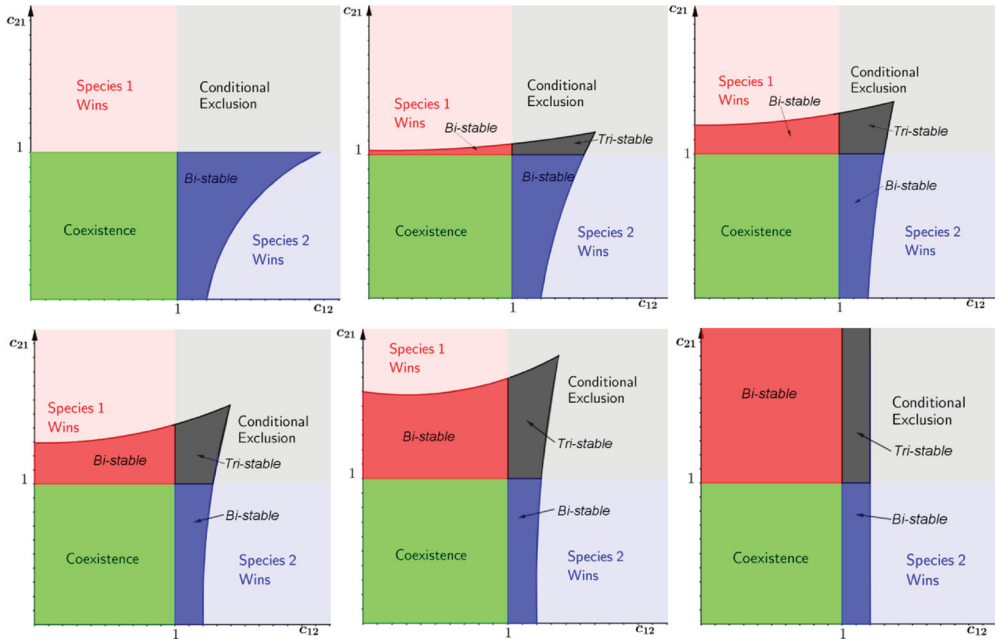


Figure 9. Competition outcomes of system (4) as function of the competitive strengths c_{12} , c_{21} for a fixed value of c_1 and increasing values of c_2 . The code colour is the same as in Figure 1 except the dark blue region that represents bi-stable conditional coexistence region in favour of species 1, dark-red region stands for bi-stable conditional coexistence region in favour of species 2 and the dark-grey region refers for the tri-stable conditional coexistence region. The figure is based on numerical calculations (the code is available in [9]) and has been edited to improve it. Parameter values are $0 < c_{12}, c_{21} < 2$, $c_1 = 1.9$ and, from left to right $c_2 = 0, 1.15, 1.65, 1.9, 6, 100, 000$.

on the initial number of individuals of each species either will coexist or one of them will go extinct. This result is straight against the classical thoughts [13,23,35], although it makes perfect sense since, how can one distinguish intra from inter species competition in so similar species?

When competition is (perfectly) asymmetric, meaning that $c_{21} = 1/c_{12}$ and that $c_2 = 1/c_1$, the classical model does not allow species coexistence, since mild competition ($c_{ij} < 1$ for $i \neq j = 1, 2$) is not possible. However, the model presented herein allows bi-stable species coexistence in favour of the lower competitor if the upper competitor expends large enough time taking resources (see Proposition 4.3). Again, this result is at odds with classical results [13,23,35] and illustrates the importance of looking carefully at how interactions take place.

Finally, we examine via numerical results the competition outcomes for the complete system (4), that are not qualitatively different from the dynamical scenarios already shown. The source code used can be found in [9].

We have found that $c_i > 0$ for $i = 1, 2$ yield the existence of bi-stable conditional coexistence regions in favour of each species (see the dark red and dark blue regions in Figure 9). The curves (that are not straight lines) delimiting such a regions are the counterparts of the curve $c_{21} = \psi_{c_1}(c_{12})$ defined by (10), that we denote by $c_{ji} = \psi_{c_i, c_j}(c_{ij})$, for $i \neq j$. Note that while $c_{21} = \psi_{c_1}(c_{12})$ is confined in the strap $(1, \infty) \times (0, 1]$, the curves $c_{ji} = \psi_{c_i, c_j}(c_{ij})$ meet on $(1, \infty) \times (1, \infty)$ defining the so-called tri-stable conditional coexistence sub-region. The classical model (1) predicts conditional exclusion due to priority effects in this region. Instead, model (4) allows species to coexist, again, provided that competitive abilities, initial values and competing time are well balanced, see Figure 9.

In words, in the strong competition scenario the mechanism(s) under the Holling type II competitive response play no role if only one of the species displays it, but facilitates coexistence when both species display it.

Note that the tri-stability region leans towards the axis c_{12} if $c_1 > c_2$ and conversely. Indeed, consider a fixed value of $c_1 > 0$ and lets see the effect of increasing c_2 (see Figure 9). As previously mentioned, a bi-stable coexistence region in favour of species 2 appears as c_2 becomes larger than 0. Besides, the bi-stable coexistence region in favour of species 1 is reduced as c_2 increases (see the panels in Figure 9). Finally, numerical experiments suggest that the bi-stable coexistence region in favour of species 1 converges to a vertical strip as $c_2 \rightarrow \infty$ (see bottom left panel in Figure 9).

Interestingly, both bi- and tri-stable conditional coexistence have been also found in the context of competition models on patchy environments with individual dispersal [25] or eco-epidemic competition models [8].

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The authors are supported by Ministerio de Economía y Competitividad (Spain), project MTM2014-56022-C2-1 and Ministerio de Ciencia, Innovación y Universidades (Spain), project RTI2018-096884-B-C32-P. H. Castillo-Alvino is also granted in the program Programa de Formación disciplinar de Docentes by the Pontificia Universidad Católica Madre y Maestra PUCMM, Dominican

Republic, to complete his Ph.D. thesis at the departamento de física y matemáticas of the universidad de Alcalá, Spain.

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