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Group defense promotes coexistence in interference competition: The Holling type IV competitive response

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Abstract

We investigate the role of group defense in the context of species interference competition by incorporating a Holling type IV like interaction term into the classical model. We have found a trade-off between species competitive strength and defense efficiency that reduces inter-species competition pressure. Thus, group defense promotes both each species probability of survival and species coexistence in two different ways: (i) Enlarging the range of parameter values yielding species survival/coexistence and (ii) Allowing for multi-stability scenarios, including global coexistence through several simultaneous coexistence asymptotically stable states that, to our knowledge, have not been previously reported in *pure* interference competition models.
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1. Introduction

Species competition is one of the main drivers of community dynamics, and it is almost ubiquitous in Nature. Key questions are whether competing species will go extinct, survive alone, or coexist and, if so, the dynamics of the resulting community [9,47]. Scientists distinguish exploitative competition from interference competition, depending on whether resource dynamics are explicit or not in the underlying model, respectively [19,42].

Exploitative competition (also resource–consumer competition) may take different forms, consisting one of them of two competing resources (or preys) and one consumer (or predator) that feeds on either one of them or both of them [17,52]. This class of models can be thought of as an interference competition model coupled to a predatory structure. In this context defense can be against competitors or predators/consumers, but only defense against consumers can be found in the literature. Competition-defense (against consumers) trade-offs have been widely analyzed, and considered for long time as a coexistence mechanism [11,24,43]. However, recent works in coexistence theory reveal that these trade-offs cannot explain coexistence by themselves, and further conditions are needed to allow long-term coexistence [9,10,20]: niche partitioning and the right balance between prey competition

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and predator pressure. Indeed, recent experimental results in consumer–resource competition suggest that defense against predators may either weaken or enhance species coexistence [45].

This work is aimed to introduce group defense in interference competition models. Interference competition takes place directly between individuals. [56] identifies four main types of interference, namely (i) reduction in foraging rate [51] (for instance, reduction in searching time or food intake rate), (ii) increased metabolic needs because of the interference activity, (iii) reduced survival rate [3,13,46] (for instance, through violent contests or aggressions), and (iv) reduced reproduction rate [32] (e.g., predation on egg or larvae, or disturbing nesting/breeding activities). This classification is not exhaustive; for instance, interference may take place also by precluding competitors physical settlement [27,53].

It is well described in the literature that species competition triggers evolution either selecting individuals with better competitive abilities [4,39] or promoting new adaptive strategies: [15,34,35], alternative life-history [33], dispersal strategies [36,41] or herd-type behavior [1,6,37], being the last one a form of group defense [30] that has been observed in both vertebrate and invertebrate animals [38]. However, group defense in interference competition may take place in a different form than the structured social defensive behavior considered in [37]. For example, the ant species *Aphaenogaster Cockerelli* and *Pogonomyrmex Barbatus* compete for seeds in the Chihuahuan desert. Before sunrise, when *P. Barbatus* colonies become active, *A. Cockerelli* colonies completely plug the nest entrances of some *P. Barbatus* colonies, thereby delaying the onset of *P. Barbatus* foraging behavior. *P. Barbatus* colonies closer to *A. cockerelli* were plugged more frequently than more distant colonies [27] (see also [53]). In addition, it has been recently proven [49] that collective action during inter-group competition in chimpanzees populations (*Pan troglodytes verus*) enhances in-group cohesion which, in the end, results in improving group survival chances.

Group defense has deserved attention in the context of predator–prey models being [16], to our knowledge, the first one. This mechanism usually modelizes predator intake rate as a one-humped function that depends on the number of prey. It means that at low prey densities the predator intake rate increases as the number of prey increases: the more prey, the more likely is to catch them. However, once population prey achieves a critical size, there are enough individuals to face predators and, thus, defend themselves. Therefore, predator intake rate decreases as the number of prey crosses this threshold value. This feature takes the general form of

$$\frac{mx}{a_0 + a_1 x + a_2 x^2}$$

and it is named after *Holling type IV functional response* [12] (but see also [29,54]). Note that this functional form was first introduced in the context of microbiology [2] and was named after Monod–Haldane functional response. Defense mechanism have been also widely analyzed in consumer–resource (i.e., exploitative) competition models [25], although defense is against consumers, and not against competitors.

Considering interaction terms different from the classical one has deserved relatively less attention in interference competition models than in predator–prey or exploitative competition models. Perhaps it is because competition systems are also competitive in the sense of [22] so that solutions converge monotonically towards an equilibrium point. However, few modifications of the classical competition model have been recently published as [6,37] where competing species display herd behavior (a type of structured group defensive behavior), or [8] were considering the time elapsed in competition leads to a competition model with the so-called Holling type II *competitive response*.

In this work, we derive an extension of the classical interference competition model [18] that incorporates a Holling type IV interference term. We have found a trade-off between species competitive strength and defense efficiency that both promotes species coexistence and allows for new dynamical scenarios that extend those found in [6,8,32] or [37]. Group defense reduces inter-species competition pressure, becoming a *stabilizing mechanism* of coexistence in the sense of [9]. New multi-stability scenarios are allowed, including multiple coexistence states. We describe all the possible competition outcomes when one of the species exhibits group defense, and provide threshold values enabling one or another outcome. We fully address the case of symmetric competition when both species display the above-mentioned feature, and numerically explore the most general case.

We discuss the impact of group defense on transient dynamics, and also describe a *jump effect* on the asymptotic behavior that may arise due to small variations on the model coefficients. Our findings may have implications in the understanding of the above-mentioned class of consumer-resource competition models.

This work is organized as follows: In Section 2 we derive the above-mentioned model. In Section 3 we assume that just one of the species displays group defense. The full system turned out to be too complex to perform a full analytical study. Thus Section 4 is devoted to the analysis of the full model under symmetric competition, and

we leave a numerical approach to the most general case to Section 5. Finally, Section 5 contains the discussion of results and final conclusions. For the convenience of the reader, the results in mathematical form have been sent to Appendix A, B, and C.

2. Deriving the Holling type IV competition model and preliminary results

The departure model is the classical Lotka–Volterra competition model [40]

$$\begin{cases} x_1' = r_1 x_1 - a_{11} x_1^2 - a_{12} x_1 x_2, \\ x_2' = r_2 x_2 - a_{22} x_2^2 - a_{21} x_1 x_2, \end{cases} \tag{1}$$

where x_i stands for the amount of individuals of species $i = 1, 2$, $r_i > 0$ is the intrinsic growth rate of species $i = 1, 2$ and $a_{ij} > 0$ the coefficient accounting for intra ($i = j$) and inter ($i \neq j$) species competition, for $i, j = 1, 2$. We considered the *emergent carrying capacities* formulation as in [48,50].

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

$$\frac{x_i'}{x_i} = r_i - a_{ii} x_i - a_{ij} x_j, \qquad i \neq j, \qquad i, j = 1, 2. \tag{2}$$

Note that the competitive pressure of a fixed number of individuals of species j on species i is the same *regardless* of the number of individuals of species i, and it would not make sense *in reality*. For instance, a fixed number of species j cannot affect the same, say, 20 or 2000 individuals of species i.

We present an alternative formulation of the classical model (1) that, essentially, is an adaptation of [28] to the current context. The first part of the exposition follows [8]: as in [23], we assume that the number N_i of competitors of species $i \neq j$ that become extinct due to the interference of *a single individual* of species $j \neq i$ within a fixed time interval T (in a fixed region) is given by

$$N_i = aT_{actv} x_i \tag{3}$$

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, etc.), a is the product of the competitors finding rate times the rate of victories of the competitor times the probability of meeting a competitor. If interference (interaction among competitors) does not take time, $T = T_{actv}$; otherwise $T > T_{actv}$. Let T_{int} be the average time that interference takes, so that $T_{actv} = T - T_{int} N_i$. Plugging this expression in (3) yields

$$N_i = aT_{actv} x_i = a(T - T_{int} N_i) x_i \tag{4}$$

that is equivalent to

$$N_i = \frac{aT x_i}{1 + aT_{int} x_i} \tag{5}$$

hat we called *Holling type II competitive response due to interference time* in [8]. We assume now that the interference time T is not constant; instead, it increases linearly with the number of individuals of species i

$$T_{int}(x_i) = (b + dx_i) T_{int} \tag{6}$$

that modelizes group defense, where b is a constant and d is the (species i) average group defense effect. Note that $d = 0$ means that assembling individuals of species i has no effect on interference time. Also, $b = 0$ means that interference time is negligible compared to group defense for species i. Using (6) in (5) leads to

$$N_i = \frac{aT x_i}{1 + abT_{int} x_i + adT_{int} x_i^2}, \tag{7}$$

that is equivalent to equation (1.31) in [28] for obvious reasons, we refer to this term as *Holling type IV competitive response due group defense*. Indeed, we assume $b = 0$ from now on. Replacing $a_{ij} x_i$, $i \neq j$, in system (1) by (7) and relabeling coefficients yields

$$\frac{x_i'}{x_i} = r_i - a_{ii} x_i - \frac{a_{ij} x_j}{1 + a_i x_i^2}, \qquad i \neq j, \qquad i, j = 1, 2, \tag{8}$$

where $a_i = adT_{int}$. Thus, the inter-species competition rate is constant only if interactions are instantaneous (i.e., $T_{int} = 0$). In other case, the effect of species j on species i is density dependent, a decreasing function of x_i^2
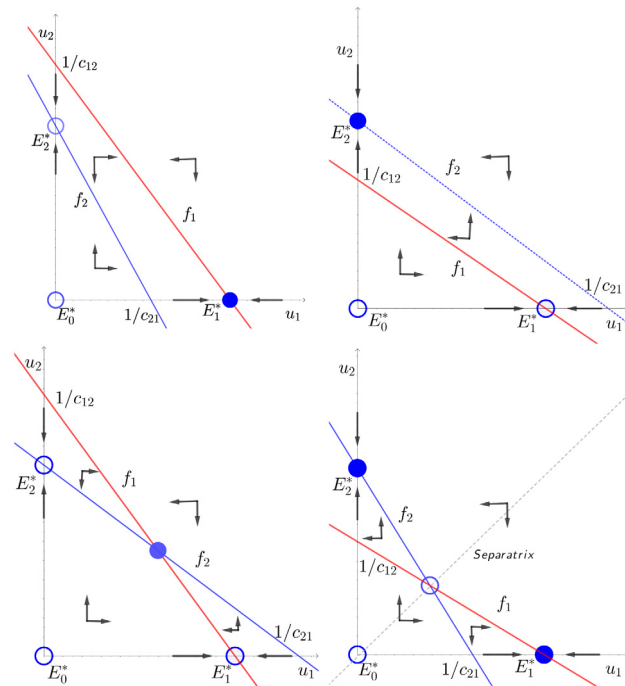
Fig. 1. Possible phase portraits of the classical competition system (system (9) with $c_i = 0$, $i = 1, 2$). The straight line f_i stands for the nullcline of species $i = 1, 2$. Solid points are asymptotically stable equilibrium points and empty points are unstable equilibria.

for a fixed amount of individuals of species j. Thus, species i population size affects the balance between intra and inter-species competition, that is key for species extinction/survival (and, thus, species coexistence) [42,55]. Letting $a_i = 0$ in (8) yield the classical per capita population growth rate (2).

Let us rewrite system (8) in a suitable way by setting $u_i = a_{ii} x_i / r_i$, $c_{ij} = a_{ij} r_j / (r_i a_{jj})$ and $c_i = a_i r_i^2 / a_{ii}^2$, that yields

$$\begin{cases} u_1' = & r_1 \left(u_1 - u_1^2 - \frac{c_{12} u_1 u_2}{1 + c_1 u_1^2} \right), \\ u_2' = & r_2 \left(u_2 - u_2^2 - \frac{c_{21} u_2 u_1}{1 + c_2 u_2^2} \right). \end{cases} \tag{9}$$

System (1) is a particular case of (9) when $c_i = 0$. Direct calculations show that system (9) is well behaved: the axes are invariant, solutions are bounded from above and the positive cone is forward invariant; the interested reader can found the result and its proof in Theorem 1, in Appendix A. Note that the flow of system (9) in the positive cone is strictly decreasing outside the rectangle $[0, 1] \times [0, 1]$. Thus, there is no equilibrium point for system (9) in $(1, +\infty) \times (1, +\infty)$.

For the convenience of the reader, we first recall the basic results on the classical competition model (1) in Table 1 (columns 1, 2 and 3; see also Figs. 1 and 2). The results are well known and can be found in [40], section 3.5. We denote $E_1^* = (1, 0)$ and $E_2^* = (0, 1)$ the so-called semi-trivial equilibrium points, that are fixed points of both system (1) and system (9). Generally, E^* would refer to a positive (meaning interior, in the positive cone) equilibrium point; there exists a closed form for E_* referred to system (1). Table 1 includes also (but not only) the stability conditions for E_1^* and E_2^* relative to system (9), that can be derived by a standard analysis of the eigenvalues of the corresponding Jacobian matrix (see Theorem 2). The acronym GAS (LAS, resp) refers to the global (local, resp) asymptotic stability of a fixed point.
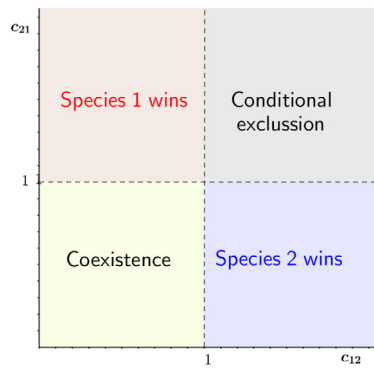
Fig. 2. Possible competition outcomes of the classical competition system (system (9) with $c_i = 0, i = 1, 2$) for different values of the competitive strength c_{12} and c_{21}.

Table 1
E_1^* and E_2^* stand for the semi-trivial equilibrium points and E^*, $E_\pm^*$ are interior (coexistence) equilibrium points. GAS (LAS, resp) stands for being global (local, resp) asymptotically stable, and unst. for unstable. Column 1 summarizes the competitive outcomes of the classical model (1) depending on competitive strengths c_{12} and c_{21} (columns 2 and 3). Column 4 displays the values of c_1 that lead to each competition outcome of system (9) in column 5.

Classical model	c_{12}	c_{21}	c_1	Holling IV model
E_1^* GAS, E_2^* unst.	$(0, 1)$	$(1, +\infty)$	$(0, +\infty)$	E_1^* GAS, E_2^* unst.
E_1^*, E_2^* LAS, E_3^* unst.	$(1, +\infty)$	$(1, +\infty)$	$(0, +\infty)$	E_1^*, E_2^* LAS, E_+^* unst.
E_1^* unst., E_2^* GAS	$(1, +\infty)$	$(0, 1)$	$(0, c_{1-}^*)$	E_1^* unst., E_2^* GAS
			$(c_{1-}^*, +\infty)$	E_1^*, E_+^* unst., E_2^*, E^* LAS
E_1^*, E_2^* unst., E_3^* GAS	$(0, 1)$	$(0, 1)$	$(0, c_{1-}^*) \cup (c_{1+}^*, +\infty)$	E_1^*, E_2^* unst., E^* GAS
			(c_{1-}^*, c_{1+}^*)	E_1^*, E_2^*, E_+^* unst., E_-^*, E^* LAS

The results summarized in Table 1 (columns 1, 2 and 3) point out 1 as a threshold value to compare with the competitive strength $c_{ij}, i \neq j$. Let us recall that the *competitive strength*

$$c_{ij} = \frac{a_{ij}/r_i}{a_{jj}/r_j} \tag{10}$$

relates intra and inter-species competition coefficient and species intrinsic growth rates (growth rates must be taken into account in order to avoid senseless results [31]). In short, species j cannot 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. It is equivalent to say that inter-species competition is lower than species i growth rate times species i intra-species competition.

We will refer to *classical coexistence* when there is a single interior GAS equilibrium point, and to *conditional extinction* or *extinction due to priority effects* when $E_i^*, i = 1, 2$ are LAS, there exists an interior unstable equilibrium point with a separatrix passing through it that defines their basins of attraction.

Let us note that the following sections include numerical simulations to either illustrate analytical results or explore those settings too complicated to be analytically analyzed. The corresponding parameter values have been chosen *ad hoc* to better illustrate the underlying mathematical result.

3. Holling type IV competitive response on just one species

We now assume that only species 1 exhibits group defense, that is, we analyze system

$$\begin{cases} u_1' = & r_1 \left(u_1 - u_1^2 - \frac{c_{12} u_1 u_2}{1 + c_1 u_1^2} \right) \\ u_2' = & r_2 (u_2 - u_2^2 - c_{21} u_1 u_2) \end{cases} \tag{11}$$
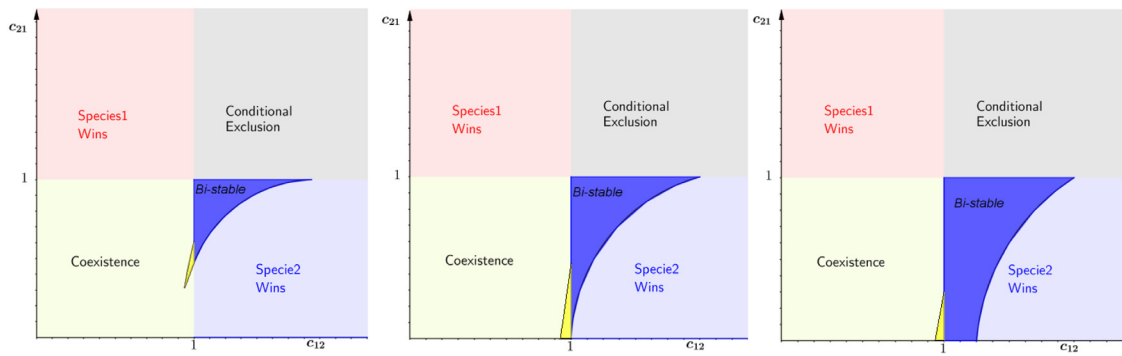
Fig. 3. Competition outcomes of system (11) as function of competitive strengths c_{12}, c_{21} for increasing values of c_1 (from left to right). The color is de same as in classical model Fig. 1 except the dark blue and the yellow regions that represent conditional coexistence (species either coexist or species 1 goes depending on the initial value, see panel (vi) in Fig Fig. 4) and global bi-stable coexistence (two coexistence equilibrium points, see panel (v) in Fig. Fig. 4). The above panels are based on numerical calculations with the code source available in [7]. The code numerically calculates the equilibrium points of the competition model for the parameter values ranging $0 < c_{12}, c_{21} < 2$ and (from left to right) $c_1 = 1.95$, 2.45, 9. Then, the stability is checked computing the eigenvalues of the Jacobian matrix at the corresponding equilibrium point. The resulting plots have been edited to improve them. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The interested reader can find the results formulated as theorems with their corresponding proofs in Appendix A. We focus on the interior (coexistence) equilibrium points by analyzing the nullclines of system (11),

$$u_2 = f_1(u_1) = \frac{1}{c_{12}}(-c_1 u_1^3 + c_1 u_1^2 - u_1 + 1), \qquad u_2 = f_2(u_1) = 1 - c_{21} u_1 \tag{12}$$

Note that $u_2 = f_2(u_1)$ is a straight line, as in the classical model. In contrast, the nullcline $u_2 = f_1(u_1)$ is a third degree polynomial. This feature is behind the differences between the outcomes of the classical model (11) and the current model. See Fig. 4 and, in particular, panels (v) and (vi) (compare to Fig. 1). Equating $f_1(u_1) = f_2(u_1)$ yields

$$P(u_1) = u_1^3 - u_1^2 + \frac{s}{c_1} u_1 - \frac{r}{c_1} = 0, \tag{13}$$

where, $r = 1 - c_{12}$ and $s = 1 - c_{12}c_{21}$. We extensively use Sturm's Theorem, that we summarize next for the convenience of the reader. Sturm's Theorem allows one to count the number of zeros of a polynomial in a given interval from the change of sign at the extremes of the interval of the so-called Sturm's sequence. The Strum's sequence associated to $P(u_1)$ is

$$Seq_p = \{P(u_1), P'(u_1), R_1(u_1), R_2(u_1)\} \tag{14}$$

where the second term is the derivative of $P(u_1)$ and $R_i(u_1)$, $i = 1, 2$, is the remainder of an euclidean division: $R_1(u_1) = -rem(P(u_1), P'(u_1))$ and $R_2(u_1) = -rem(P'(u_1), R_1(u_1))$. We already know that any interior fixed point of (9) is on $[0, 1] \times [0, 1]$. Let $V(\hat{u}_1)$ stand for the number of sign changes in the terms of the sequence (14) at $u_1 = \hat{u}_1$. Then, $V(0) - V(1)$ yields the number of real roots of $P(u_1)$ in $[0, 1]$.

Most terms in $V(0)$ and $V(1)$ have constant sign. Direct calculations show that $V(0) - V(1)$ depends on whether c_{12} and c_{21} are smaller or larger than 1 and on the relative size of c_1 to the threshold values $c_{1\pm*}$ defined by

$$c_{1\pm}^* = \frac{27r^2 - 18sr - s^2 \pm \sqrt{(r-s)(9r-s)^3}}{8r} \tag{15}$$

that results from solving $R_2(1) = 0$ in c_1. The possible competition outcomes are summarized in Table 1, see also Fig. 3. In addition, Fig. 4 displays all the possible phase portrait configurations of system (11).

It is apparent that system (11) allows for two new dynamical scenario (compared to the classical system (1)):

- *Conditional coexistence (of type I) in favor of species 1*, that arises when E_2^* is LAS, E_2^* unstable, there exist a positive LAS equilibrium point E_+^*, and a positive unstable equilibrium point E_+^* whose stable manifold
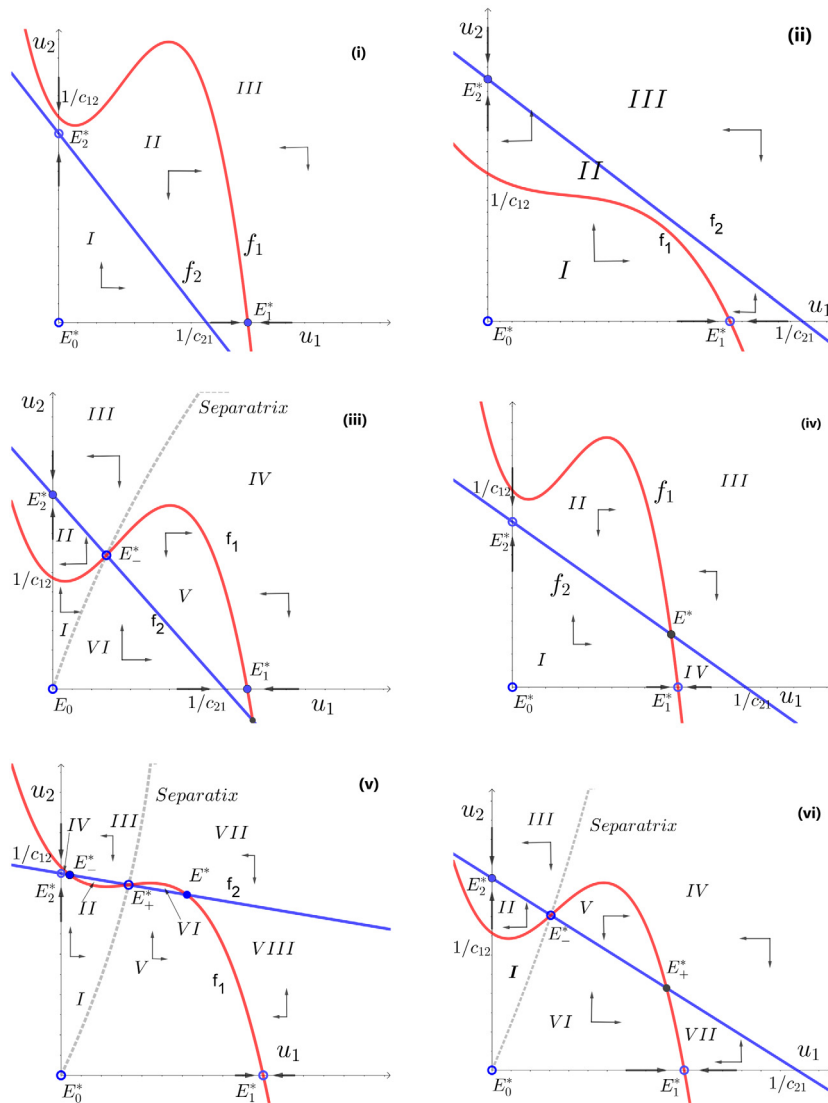
Fig. 4. Possible phase portraits of system (11) with competitive response just in species 1 ($c_2 = 0$). The curve f_i stands for the nullcline of species $i = 1, 2$. The parameter ranges leading to each scenario are summarized in Table 1. From top to down, from left to right, panels correspond to rows 1, 3, 2, 5, 6 and 4 in Table 1, respectively. Parameter values (i) $(c_1, c_{12}, c_{21}) = (6.7, 0.92, 1.28)$, (ii) $(c_1, c_{12}, c_{21}) = (2.5, 1.64, 0.77)$, (iii) $(c_1, c_{12}, c_{21}) = (8.7, 1.751.13)$, (iv) $(c_1, c_{12}, c_{21}) = (6, 0.84, 0.71)$, (v) $(c_1, c_{12}, c_{21}) = (3.35, 0.97, 0.17)$, (vi) $(c_1, c_{12}, c_{21}) = (6.7, 1.4, 0.63)$.

defines a separatrix that delimits the basins of attraction of E_2^* and E^*. It happens for $c_{12} > 1$, $0 < c_{21} < 1$ and $c_1 > c_{1-}^*$, see panel (vi) in Fig. 4, Table 1 and Theorem 5.

- *Global bi-stable coexistence* arises when E_1^* and E_2^* are unstable, there exist two interior LAS equilibrium points E_-^* and E^*, and another interior unstable equilibrium point E_+^* whose stable manifold defines a separatrix that delimits the basins of attraction of E_-^* and E^*. It happens when $0 < c_{12} < 1$, $0 < c_{21} < 1$ and $c_{1-}^* < c_1 < c_{1+}^*$, see Table 1. See the last row in Table 1, panel (v) in Fig. 4 and Theorem 6.

In the overall, the long term behavior of system (11) is the same as the classical model (1) for $c_{21} > 1$ although there are quantitative differences as $c_1 > 0$, see Sections 5.1 and 5.2. In addition to the quantitative differences, qualitatively new scenarios may appear for $0 < c_{21} < 1$. See Section 5.2 for further details.

4. Holling type IV competitive response on both species

In this section, we focus on the complete model (9) by assuming that both species exhibit group defensive behavior. We already know that system (9) is well behaved (see Theorem 3) and we seek for the existence and stability of the positive equilibrium points. The nullclines of system (9) are third degree polynomials defined by

$$u_2 = f_1(u_1) = \frac{1}{c_{12}}(-c_1 u_1^3 + c_1 u_1^2 - u_1 + 1), \qquad u_1 = f_2(u_2) = \frac{1}{c_{21}}(-c_2 u_2^3 + c_2 u_2^2 - u_2 + 1) \tag{16}$$

so that the positive equilibrium points are given by the positive roots of

$$P(u_1) = \frac{1}{c_{12}^3 c_{21}} \sum_{k=0}^{9} \gamma_k u_1^k = 0, \tag{17}$$

where

$$
\begin{array}{ll}
\gamma_9 = c_1^3 c_2 & \gamma_8 = -3c_1^3 c_2 \\
\gamma_7 = 3c_1^2 c_2 (1 + c_1) & \gamma_6 = c_1^2 c_2 (c_{12} - c_1 - 9) \\
\gamma_5 = c_1 c_2 [c_1 (9 - 2c_{12}) + 3] & \gamma_4 = c_1 c_2 [c_1 c_{12} - 3c_1 + 2c_{12} - 9] \\
\gamma_3 = c_{12} c_1 (c_{12} - 4c_2) + c_2 (9c_1 + 1) & \gamma_2 = c_{12} [c_2 (1 + 2c_1) - c_1 c_{12}] - 3c_2 (c_1 + 1) \\
\gamma_1 = c_{12}^2 (1 - c_{12} c_{21}) + c_2 (3 - 2c_{12}) & \gamma_0 = (c_{12} - 1)(c_{12}^2 + c_2)
\end{array}
\tag{18}
$$

Unfortunately, equation $P(u_1) = 0$ is too involved to get any biological insight, and it is numerically explored in Section 5.3. However, analytical results can be obtained in the following particular case.

4.1. Symmetric competition

Typically, symmetric competition takes place between individuals of different species with similar phenotypic traits [26,57]. Thus, we set the competitive strengths and the group defense coefficients as

$$c_{12} = c_{21} \equiv c_{\bullet\bullet} \qquad\qquad c_1 = c_2 \equiv c_\bullet \tag{19}$$

In such a case, Eq. (17) can be written as:

$$P(u_1) = \frac{1}{c_{\bullet\bullet}^4} g(u_1) h(u_1), \tag{20}$$

where,

$$g(u_1) = c_\bullet u_1^3 - c_\bullet u_1^2 + (1 + c_{\bullet\bullet}) u_1 - 1 \tag{21}$$

and

$$
\begin{aligned}
h(u_1) = \;& c_\bullet^3 u_1^6 - 2c_\bullet^3 u_1^5 + \left[c_\bullet^3 + c_\bullet^2 (2 - c_{\bullet\bullet}) \right] u_1^4 \\
& - 2c_\bullet^2 (2 - c_{\bullet\bullet}) u_1^3 + \left[c_\bullet^2 (2 - c_{\bullet\bullet} + c_\bullet (c_{\bullet\bullet}^2) - c_{\bullet\bullet} + 1) \right] u_1^2 \\
& - (c_{\bullet\bullet}^2 - 2c_{\bullet\bullet} + 2) u_1 + (c_\bullet + c_{\bullet\bullet}^2 - c_\bullet c_{\bullet\bullet} - c_{\bullet\bullet}^3)
\end{aligned}
\tag{22}
$$

The main analysis tool is, again, the Sturm's Theorem applied to the $g(u_1)$ and $h(u_1)$ (defined in (21) and (22)) in the polynomial Eq. (20). A precise theorem formulation along with a rigorous proof can be found in Theorem 7 in Appendix C. A summary of the results can be found in Table 2 and Figs. 5 and 6.

We compute the number of change of signs of the Sturm's sequence of polynomial (20) at $u_1 = 0, 1$ as in Section 3. In this case, we do so through Sturm's sequences of (21) and (22) denoted by

$$Seq_g = \{ g(u_1), g'(u_1), R_1(u_1), R_2(u_1) \} \tag{23}$$

$$Seq_h = \{ h(u_1), h'(u_1), T_1(u_1), T_2(u_1), T_3(u_1), T_4(u_1), T_5(u_1) \} \tag{24}$$

Many terms in these sequences have constant sign at $u_1 = 0, 1$. It also turns out that $R_2(u_1), T_4(u_1), T_5(u_1)$ may display different sign at $u_1 = 0, 1$ depending on the value of $c_\bullet$ and $c_{\bullet\bullet}$. Solving the corresponding equations on $c_\bullet$ yield threshold values defined by

$$c_{\bullet\pm}^{**}(c_{\bullet\bullet}) = \frac{-3c_{\bullet\bullet}^2 + 20c_{\bullet\bullet} - 8 \pm \sqrt{c_{\bullet\bullet}(9c_{\bullet\bullet} - 8)(c_{\bullet\bullet} + 8)^2}}{8} \tag{25}$$

Table 2

Classification of competition outcomes of system (9) under symmetry conditions (19) as function of $c_{\bullet\bullet}$ and $c_{\bullet}$.

| Competition outcome	Competitive strength $c_{\bullet\bullet}$	Defense coefficient $c_{\bullet}$
Classical global coexistence	$c_{\bullet\bullet} \in \left(0, \frac{8}{9}\right)$	$c_{\bullet} \in (0, +\infty)$
Classical global coexistence	$c_{\bullet\bullet} \in \left(\frac{8}{9}, 1\right)$	$c_{\bullet} \in (0, c_{\bullet-}^{**}) \cup (c_{\bullet+}^{**}, +\infty)$
Bi-stable global coexistence		$c_{\bullet} \in (c_{\bullet-}^{**}, c_{\bullet+}^{**})$
Tri-stable global coexistence		$c_{\bullet} \in (c_{\bullet+}^{**}, c_{\bullet}^{***})$
Conditional coexistence type I	$c_{\bullet\bullet} \in (1, 8)$	$c_{\bullet} \in (0, c_{\bullet+}^{*}) \cup (0, c_{\bullet+}^{*})$
Conditional exclusion type I		$c_{\bullet} \in (c_{\bullet+}^{**}, +\infty)$
Conditional exclusion type I	$c_{\bullet\bullet} \in (8, \hat{c}_{\bullet\bullet})$	$c_{\bullet} \in (0, c_{\bullet-}^{*}) \cup (c_{\bullet+}^{*}, c_{\bullet+}^{**})$
Conditional exclusion type II		$c_{\bullet} \in (c_{\bullet-}^{*}, c_{\bullet+}^{*})$
Conditional coexistence type I		$c_{\bullet} \in (c_{\bullet+}^{**}, +\infty)$
Conditional exclusion type I	$c_{\bullet\bullet} \in (\hat{c}_{\bullet\bullet}, +\infty)$	$c_{\bullet} \in (0, c_{\bullet-}^{*})$
Conditional exclusion type II		$c_{\bullet} \in (c_{\bullet-}^{*}, c_{\bullet+}^{**})$
Conditional coexistence type II		$c_{\bullet} \in (c_{\bullet+}^{**}, c_{\bullet+}^{*})$
Conditional coexistence type I		$c_{\bullet} \in (c_{\bullet+}^{*}, +\infty)$
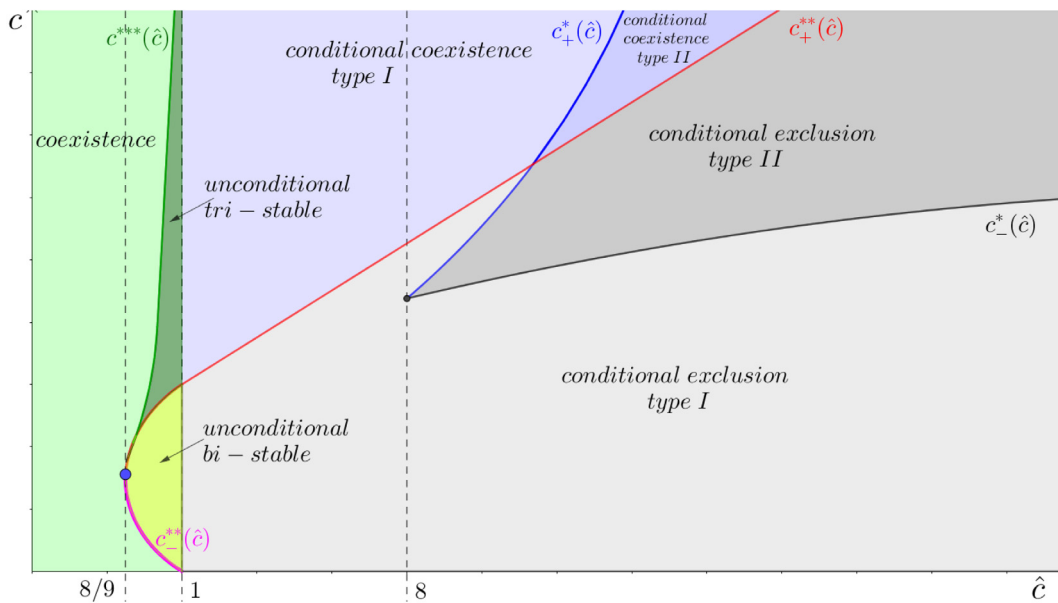
Fig. 5. Classification of system (9) competition outcomes under symmetry conditions (19) as a function of $c_{\bullet\bullet}$ and $c_{\bullet}$. In green: global species coexistence (light — classical, yellow — bi-stable, dark — tri-stable). In purple: species conditional coexistence (light — type I, dark — type II). In gray: species conditional exclusion (light — type I, dark — type II). The figure has been computed as described at the foot of Fig. 3. Parameters range: $0 < \hat{c} < 200$ and $0 < c < 50$. Note that we have used a free scale in both axis to better display the main features. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$$c_{\bullet\pm}^{*}(c_{\bullet\bullet}) = \frac{c_{\bullet\bullet}^{2} + 20c_{\bullet\bullet} - 8 \pm \sqrt{c_{\bullet\bullet}(c_{\bullet\bullet} - 8)^{3}}}{8} \tag{26}$$

$$c_{\bullet}^{***}(c_{\bullet\bullet}) = -\frac{13c_{\bullet\bullet}^{2} + \sqrt{c_{\bullet\bullet}(8 - 7c_{\bullet\bullet})^{3}} - 4c_{\bullet\bullet} - 8}{8(c_{\bullet\bullet} - 1)} \tag{27}$$

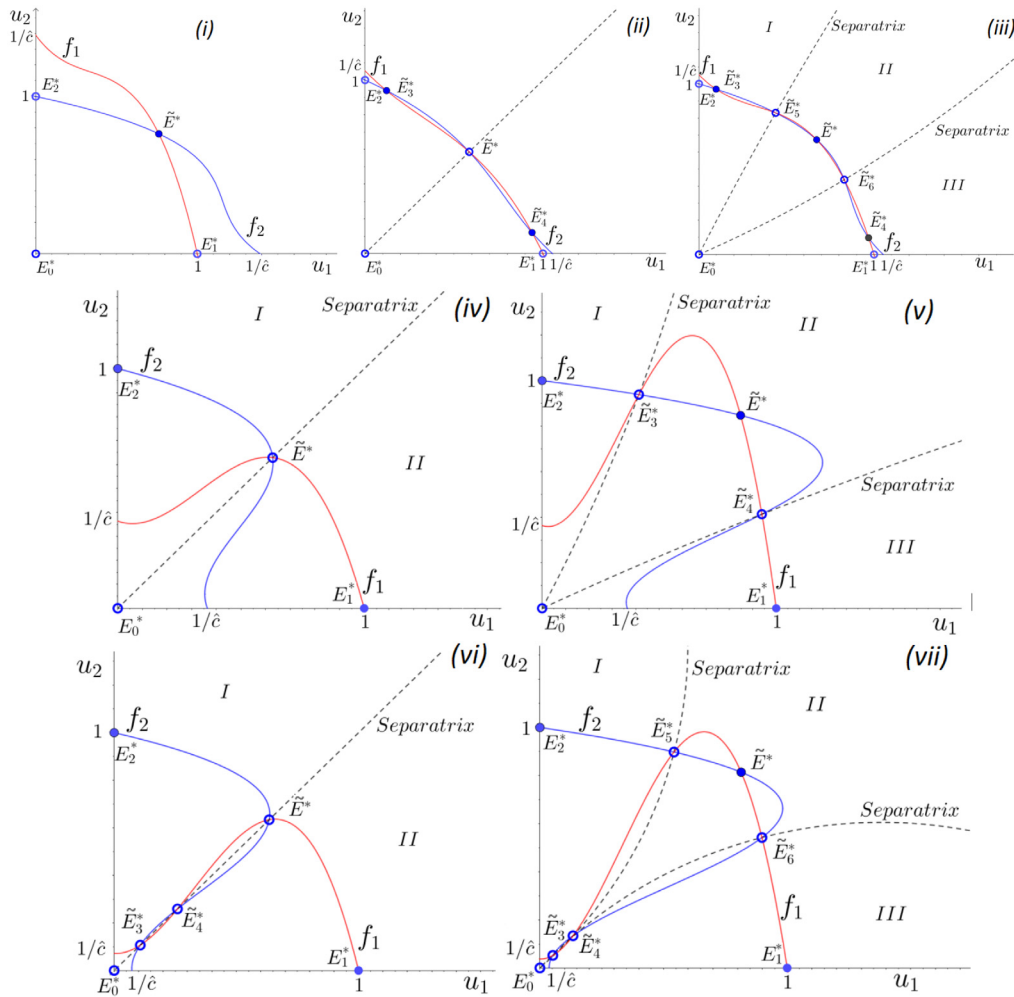for the sign of the above mentioned terms that determine the competition outcome.

Fig. 6. Possible phase portraits of system (9) under symmetry conditions (19) as function of $c_{\bullet\bullet}$ and $c_{\bullet}$. The curve f_i stands for the nullcline of species $i = 1, 2$. Note that panels (iv) and (vi), and (v) and (vii) display essentially the same dynamical outcome, but the number of unstable equilibrium points makes each of them mathematically different from the other ones. Parameter values: (i) $(\hat{c}, c) = (0.95, 0.5)$, (ii) $(\hat{c}, c) = (0.95, 1.4)$, (iii) $(\hat{c}, c) = (0.95, 2.5)$, (iv) $(\hat{c}, c) = (0.95, 3.25)$, (v) $(\hat{c}, c) = (45, 7)$, (vi) $(\hat{c}, c) = (50, 13)$, (vii) $(\hat{c}, c) = (122.5, 22)$. Parameter values have been chosen *ad hoc* to illustrate the possible nullclines configuration, and may have no ecological sense.

Interestingly, and despite the fact that solutions converge monotonically to an equilibrium point [22], we have found 6 qualitatively different outcomes, as there are up to 7 interior equilibrium points in the positive cone. Thus, there are new asymptotic behaviors different from those of the classical model (classical coexistence, conditional exclusion, one species extinction) and those found when considering group defense in just one species (conditional coexistence in favor of species 1 and global bi-stable coexistence). Namely:

- *Conditional extinction of type II*: E_i^*, $i = 1, 2$ are LAS, there exist 2 interior unstable equilibrium points and a separatrix passing through them that define their basins of attraction, see panel (vi) in Fig. 6 (we refer to type I if there is 1 interior unstable fixed point, as in panel (iv), Fig. 6).
- *Bi-stable global coexistente* (resp., *tri-stable global coexistence*): semi-trivial equilibrium points are both unstable and there are 2 LAS interior equilibrium points (resp., 3 LAS interior fixed points). There exists also an interior unstable equilibrium point (resp., 2 unstable interior fixed points) and a separatrix passing through it that defines their basins of attraction; see panel (ii) in Fig. 6 (resp., see panel (iii) in Fig. 6).

- *Conditional coexistence*: the semi-trivial equilibrium points are both stable, and there is also a LAS interior equilibrium points. There exist 2 (type I; or 4, type II) interior unstable equilibrium points and separatrices passing through each of them that define the basins of attraction. Coexistence or one species extinction depends on priority effects (the initial amount of individuals of each species). See panels (v) and (vii) in Fig. 6.

It is worth noting that symmetric competition conditions preclude global extinction of one of the species, implying that E_i^*, $i = 1, 2$, cannot be GAS. We have included here type I and type II scenarios for the sake of completeness. In the overall, these two outcomes do not really differ from each other, just in the transient dynamics and for values close to the origin. We leave comments and interpretations to Section 5

5. Discussion and conclusions

In the overall, we have found that group defense strategy improves the chances of coexistence, mainly by lowering the inter-species competition effect with respect to intra-species pressure. This mechanism can be added to cooperation–competition effects [55] or the time taken in interference [8] as mechanisms enhancing coexistence, all of them belonging to the so-called *stabilizing* mechanisms of coexistence [9].

In consumer-resource competition, the stronger competitor is also more "exposed" to consumers, which reduces their competitive strength by feeding on them. Group defense has been widely considered in this context, although defense is against consumers and not against competitors. Consumer-resource models estate a trade-off between resource defense (against consumer) and resource growth [14,25], meaning that species should prioritize one of these strategies. In contrast, such a dichotomy does not hold in interference competition, since defending against competitors relaxes inter-species pressure enabling stronger growth.

Also, group defense (against consumers) may either weaken or enhance species coexistence in exploitative competition [45] by deflecting consumer pressure to the other resource species. Interestingly, we have found that group defense does not weaken, in any case, the chance of coexistence in interference competition.

The role of group defense (against competitors) may play a key role in consumer–resource dynamics, since enabling resource species coexistence implies sharing consumer pressure. That is, in complex community dynamics bringing competitors to extinction may not always be the best idea. It would be of interest to explore possible trade-offs between-group defense against competitors, group defense against consumers, and consumers' pressure on resources.

Empirical observations support multiple stable coexistence states [21] in species competing by interference. The proposed mechanism in [21] relies on fast–slow coupled processes. To our knowledge, interference competition models that allow for multiple coexistence states have been reported in the context of slow–fast systems when the competition models incorporate another (relatively fast) process, such as disease dynamics [44] or individual dispersal [36], but not in a *pure* interference competition model, as the one presented herein.

5.1. Group defense and nullclines

Whether competing species manage to coexist or not depends on the balance between intra and inter-species competition [42,55]; see comments after expression (10). We first analyze how group defense impacts on this balance. Fig. 7 displays the nullcline f_1 for species 1 of system (9).

The nullcline $u_2 = f_1(u_1)$ bounds the region R_1 where species 1 has positive growth (see Fig. 7) and defines the minimal population 2 size that prevents population 1 to keep growing. In the classical model ($c_1 = 0$, left panel in Fig. 7) $f_1(u_1) = (1 - u_1)/c_{12}$ is a straight line with negative slope, and the smaller is the competitive strength c_{12}, the larger is R_1. This feature is due to the fact that as c_{12} decreases (see (10)), intra-species competition becomes stronger than inter-species competition. Also, regarding R_1, species 1 is less tolerant to species 2 as species 1 population size increases, meaning that the larger is the number of individuals of species 1, the less tolerant (in order to keep growing) is to species 2.

However, as c_1 becomes positive f_1 is not a straight line anymore (center and right panels of Fig. 7) and R_1 becomes larger because group defense reduces the effect of inter-species competition on species 1. Direct calculations yield that $f_1(0) = 1/c_{12}$, $f_1'(0) < 0$, and there is a inflection point at $u_1 = 1/3$. Furthermore, there exist local extrema at $0 < \hat{u}_{1-} < \hat{u}_{1+} < 1$ for $c_1 > 3$ (see right panel of Fig. 7).
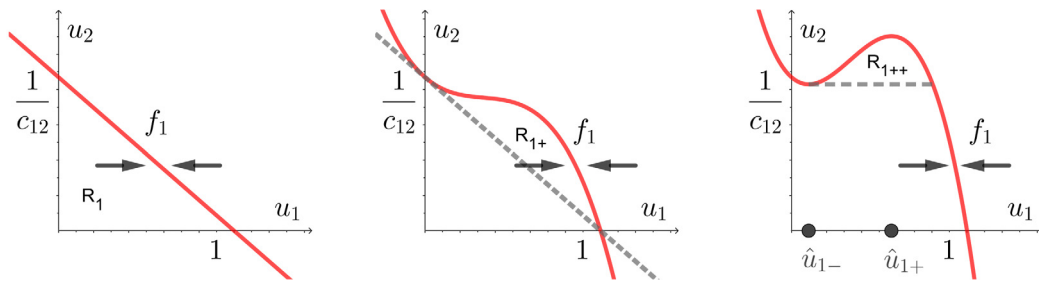
Fig. 7. The nullcline $u' = 0$ of system (9) for increasing values of c_1. Left, $c_1 = 0$ (i.e., the classical Lotka–Volterra model (1); center, $c_1 \in (0, 3)$ and right, $c_1 > 3$.

Group defense is not fully active for $0 < c_1 < 3$ (center panel of Fig. 7). Namely, species 1 becomes more tolerant to species 2 because of a relative reduction of inter-species pressure (see region R_{1+} in the central panel of Fig. 7). Indeed, as $c_1 > 3$, group defense is fully active and allows species 1 to keep growing even in the presence of a larger amount of individuals of species 2 than before ($u_1 < \hat{u}_{1-}$) see region R_{1++} in the right panel of Fig. 7. In this region, a larger number of individuals of species 1 results in tolerating even a larger number of individuals of species 2. Thus, group defense somehow balances the relative weight of intra and inter-species competition on species 1.

The time elapsed in interference was considered in [8], and the corresponding nullclines are similar to those obtained for $0 < c_1 < 3$. However, the nullclines founded there were strictly decreasing regardless of the time elapsed in interference.

[6,32,37,55], on the other hand, dealt with various modifications of the classical interference competition system. There, the shape of the nullcline of species 1 is similar to $u_2 = \hat{f}_1(u_1) = au_1(1 - u_1)$. Thus, at low species 1 population size, increasing the number of individuals of species 1 results in tolerating a larger number of individuals of species 2. This feature holds until the nullcline reaches its maximum, and it is reversed from the maximum on. Note that in these works $\hat{f}_1(0) = 0$ crosses the origin whereas in the defense group case $f_1(0) = 1/c_{12} > 0$. Therefore, group defense is by far much convenient to species 1 than other strategies considered in the above-mentioned works.

5.2. Holling type IV competitive response in one species

We focus now on system (11). Two competition outcomes not allowed by the classical model arise: conditional coexistence in favor of species 1 and bi-stable global coexistence. Also, and in any case, group defense has an impact on both transient dynamics and the long-term relative size of the competing species.

In general, group defense enhances quantitatively the species displaying it. For instance, Fig. 8 displays a global coexistence scenario for two values of c_1, and it is apparent that the number of individuals of species 1 increases as c_1 increases, and conversely for species 2

We have found that system (11) with $c_{21} > 1$ yields qualitatively the same outcomes as in the classical system. However, group defense plays a role in two different ways:

- When in addition $0 < c_{12} < 1$ both the classical model and system (11) predict species 2 extinction. However, species 2 will fade away much faster due to the group defense term.
- Besides, if also $c_{12} > 1$, both the classical model and system (11) predict species extinction due to priority effects. In this case, the larger is c_1, the wider is the basins of attraction of E_1^*. That is to say species 1 is more likely to survive since it can rule out species 2. Thus, there is a trade-off between competition and defense that clearly favors coexistence, which is not always the case in exploitative competition [45].

For $0 < c_{21} < 1$ competition outcomes may be different from those in the classical system depending on the value of $c_1 > 0$. Condition $0 < c_{21} < 1$ implies that species 1 cannot drive species 2 to extinction, but species 1 can be ruled out. At this point, any defense strategy in species 1 should be key to survive, and system (11) allows so in two different ways:
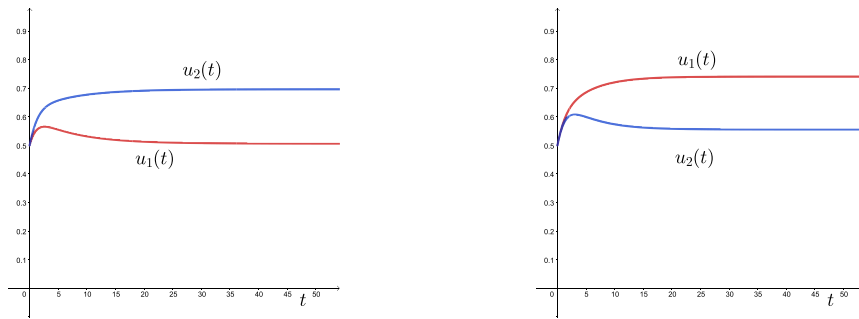
Fig. 8. When species coexist, group defense may decide which one is the dominant competitor. Left panel, $c_1 = 1.1$, $c_2 = 0$, right panel $c_1 = 2.5$, $c_2 = 0$.
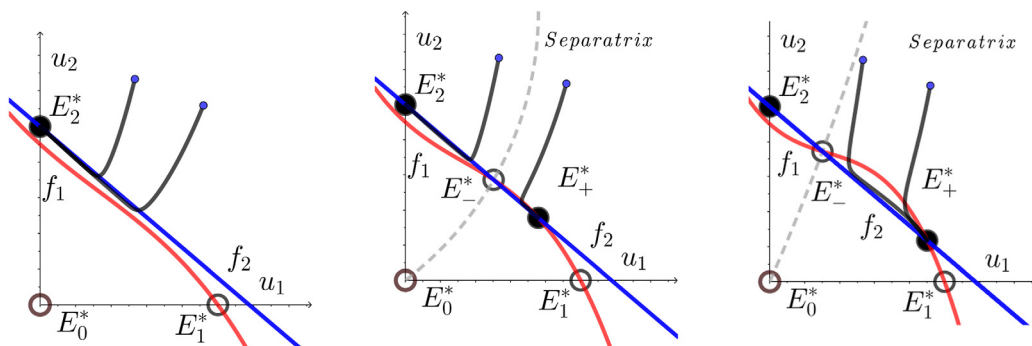

Fig. 9. Phase portraits of system (11). The straight blue line is the nullcline f_2, the curved red line is the nullcline f_1. Solid (empty, resp.) points are LAS (unstable, resp.) equilibrium points. The black curve is the orbit of an arbitrary solution of system (11). Parameter values: $c_{12} = 1.11$, $c_{21} = 0.85$, and $c_1 = 0.5$, 1.1, 2 increases from the left to the right panel.

- On the one hand, if $c_{12} > 1$, the classical model predicts species 1 extinction. However, a large enough defense coefficient $c_1 > c_{1-}^*$ allows species coexistence (in particular, species 1 to survive) via a saddle–node bifurcation (see right panel in Fig. 9). Still, E_2^* is LAS, and species 1 survival depends on the initial values. Species 1 will fade out (see left and central panels in Fig. 9) if defense is as weak as $0 < c_1 < c_{1-}^*$.
- On the other hand, if $0 < c_{12} < 1$, the classical model predicts global species coexistence via a GAS positive equilibrium point E^*. System (11) also allows global coexistence (left or right panel in Fig. 10) as in the classical model. Interestingly, moderate values of $c_1 \in (c_{1-}^*, c_{1+}^*)$ lead to a saddle–node bifurcation that leads also to global coexistence but via two LAS equilibrium points $E_{\pm}^*$ whose basins of attraction are defined by a separatrix through an unstable equilibrium point E_+^* (center panel in Fig. 10).

  Note that numerical experiments show that for $c_1 < c_{1-}^*$ the unique GAS positive equilibrium point is closer to the vertical axis than for $c_1 > c_{1+}^*$. Thus, as c_1 increases, it pulls E^* towards the horizontal axis, that means the u_1 (the u_2, resp) component of E^* increases (decreases, resp.) as c_1 increases. This behavior, however, is not smooth: as c_1 crosses the threshold value c_{1-}^* a saddle–node bifurcation takes place (center panel in Fig. 10) resulting in the above mentioned bi-stable coexistence scenario. As a result, a region of initial values in the phase plane will lead to E_+^* (in favor of u_1), while these initial values would have lean to E^* (in favor of u_2) for slightly lower values of c_1.

In [21], two alternative stable states have been described for a diverse variety of terrestrial and near terrestrial ecosystems. It is suggested that periodic changes from one state to another are mediated by changes in slow processes that suddenly trigger a fast process (that results in a response or escape from a state). We have shown that global bi-stable coexistence may arise when one (11) or both (9) competing species exhibit Holling type IV competitive response. An alternative explanation is that a sudden (stochastic-like) change in the number of
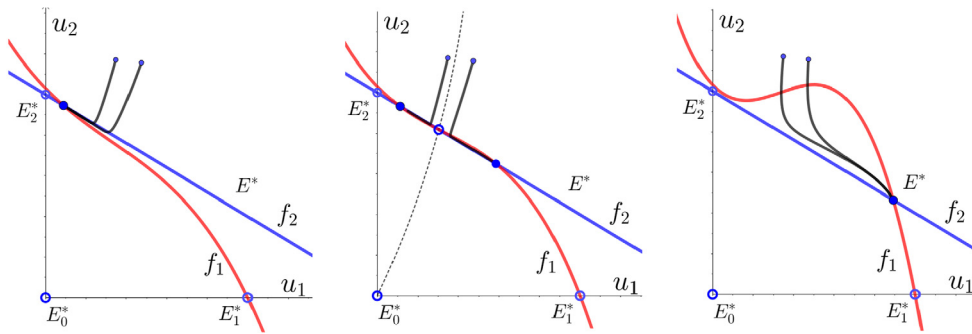
Fig. 10. Phase portraits of system (11). The straight blue line is the nullcline f_2, the curved red line is the nullcline f_1. Solid (empty, resp.) points are LAS (unstable, resp.) equilibrium points. The black curve is the orbit of an arbitrary solution of system (11). Parameter values: $c_{12} = 0.97$, $c_{21} = 0.6$, and $c_1 = 1, 1.51, 4$ increases from the left to the right panel.
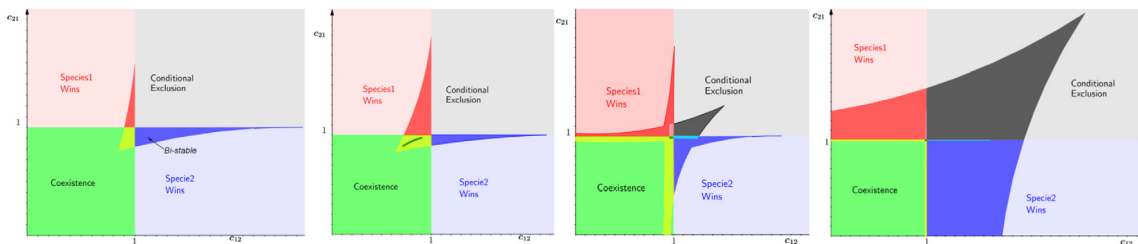

Fig. 11. Competition outcomes of system (9) as function of competitive strengths c_{12}, c_{21} for increasing values of c_1 and c_2 (from left to right). The color is the same as Fig. 3 except the dark blue, pink and cyan color's regions that represent tri-stable conditional coexistence, the dark red region stands for bi-stable conditional coexistence region in favor species 2 and the dark-green area stands for unconditional coexistence with three nontrivial equilibrium points are globally asymptotically stable. The figure has been computed as described at the foot of Fig. 3, parameter values $0 < c_{12}, c_{21} < 4$ and $(c_1, c_2) \in \{(1.9, 1.5), (3.8, 4.4), (5.8, 6.4), (15, 10)\}$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

individuals may lead the community from the basins of attraction of one of the coexistence equilibrium points to the other one. Also, competitive abilities or species strategies may change in time, for instance, due to climate fluctuations, which may result in a sequence of readjustments that pull the system from one coexistence scenario to the other one (left and right panels in Fig. 10).

5.3. Group defense competitive response in both species

Surprisingly, the full analysis of the model has turned out to be beyond the scope of this work. Note that even assuming symmetric competition, which entails serious restrictions in coefficients, has yielded a bunch of new dynamical scenarios.

Species growth rate, competitive abilities (and, thus, the corresponding competitive strength), and group defense coefficient may change in time due to several factor such as global change [5], evolution [4,39] or adaptive strategies [15,34,35]. As a result, we should not consider Figs. 2 and 3 to be static objects. The regions depicted there refer to the asymptotic behavior of the model. Thus, variations in the model coefficients taking place in the transient time may lead the community from one region to another.

There may exist up to 9 equilibrium points in the positive cone (see Eq. (17)). We have numerically explored and classified the possible equilibrium points of system (9). Fig. 11 displays the number of equilibrium points and its stability in the $c_{12} - c_{21}$ parameter plane for fixed values c_i, $i = 1, 2$. System (9) allows for the same competition outcomes as in the classical model, that are colored the same as in Fig. 1 and, besides, new competition outcomes have been found:

- *Bi-stable global coexistence* consisting of two interior LAS equilibria plus both semi-trivial equilibrium points being unstable. See the light green region in Fig. 11.
- *Tri-stable conditional coexistence in favor of one species* consisting of two interior LAS equilibria plus one of the semi-trivial equilibrium points being also LA. See the pink and the cyan regions in panels (iii) and (iv) in Fig. 11.
- *Tri-stable of conditional coexistence* consisting of one interior LAS equilibria plus both semi-trivial equilibrium points being also LAS. See the dark black region in Fig. 11.
- *Bi-stable conditional coexistence region in favor species 1 (species 2, resp)* consisting of one interior LAS equilibria and one of the semi-trivial equilibrium points being also LAS. See the dark blue (dark red, resp) region in Fig. 11
- *Global tri-stable coexistence* consisting of three nontrivial equilibrium points are LAS, while the semi-trivial equilibrium points are unstable. See the dark-green region in the coexistence square $[0, 1] \times [0, 1]$ in panels (ii), (iii) and (iv) (the last one, almost invisible) in Fig. 11.

Compared to other interference competition models, the differences are not only in how likely coexistence is, but also in the number of different scenarios are allowed by the model. Essentially, [8,37,55] allow for all the classical outcomes along with conditional coexistence in favor of one species and conditional coexistence. In contrast, system (9) may display all the previous scenarios and, in addition, global multi-stable coexistence scenarios.

Finally, we briefly depict future work, that will include parameterizing real populations to ascertain its real-world applied usefulness. The interplay between group defense and disease effects (disease modified competition) in competition models will be analyzed. Also, possible trade-offs between prey species group defense and a specialized predator deserve being analyzed.

Acknowledgments

Appendix A

Theorem 1.   *Consider system* (9). *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 axes, say $(u_1(t_0), u_2(t_0)) = (u_{01}, 0)$ becomes an uncoupled system consisting 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 direct consequence of 1 and 2.   ∎

Theorem 2.   *Consider system* (9) *with* $c_i > 0, i = 1, 2$ *and* $r_i > 0, i = 1, 2$. *Then,*

1. *The trivial equilibrium point* $E_0^* = (0, 0)$ *is unstable.*
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, $j = 1, 2$ *and* $i \neq j$.
    (b) E_i^* *is unstable stable if* $c_{ji} < 1$, i, $j = 1, 2$ *and* $i \neq j$.

Proof. The existence of E_i^*, $i = 0, 1, 2$ follows from direct calculation. The stability conditions follow from a standard analysis of the eigenvalues of the Jacobian matrix. ∎

Appendix B

Theorem 3 (*Specie* 1 *Wins*). *Consider system* (11) *with* $c_1 > 0$ *and the semi-trivial equilibrium points* E_1^* *and* E_2^*. *Then, for any solution with initial values in the positive cone,* E_1^* *is globally asymptotically stable and* E_2^* *is unstable if* $c_{21} > 1$ *and* $0 < c_{12} < 1$.

Proof. Without loss of generality, we assume $i = 1$. Consider the nullclines (28) of system (11),

$$f_1(u_1) = \frac{1}{c_{12}}(-c_1 u_1^3 + c_1 u_1^2 - u_1 + 1), \qquad f_2(u_1) = 1 - c_{21} u_1 \tag{28}$$

We look for the positive solutions of equation $f_1(u_1) = f_2(u_1)$, that are the positive roots of the third-degree equation

$$P(u_1) = u_1^3 - u_1^2 + \frac{s}{c_1} u_1 - \frac{r}{c_1} = 0 \tag{29}$$

where,

$$r = 1 - c_{12} \quad and \quad s = 1 - c_{12} c_{21}.$$

Applying the Sturm's Theorem we obtain the Strum's sequence (14) that reproduces next

$$Seq_p = \{P(u_1), P'(u_1), R_1(u_1), R_2(u_1)\}$$

Direct calculations show that $V(0) - V(1)$ (see comments after expression (14)) depends on the sign of $R_2(1)$. Solving $R_2(1) = 0$ on c_1 yields expression (15) that we reproduce for the convenience of the reader

$$c_{1\pm}^* = \frac{27r^2 - 18sr - s^2 \pm \sqrt{(r-s)(9r-s)^3}}{8r} \tag{30}$$

where

$$r = 1 - c_{12} \quad and \quad s = 1 - c_{12} c_{21}.$$

It follows that $(r - s)(9r - s)^3 < 0$ implies the existence of a real root. Besides, as $f_1(1) > f_2(1)$ and $f_1'(u_1) < 0$, $f_2'(u_1) = -c_{12}$, $f_1(u_1)$ and $f_2(u_1)$ strictly decrease for $u_1 \in (0, \infty)$, then, this real root is in the fourth quadrant.

Thus, the configuration of the phase portrait is as in the first row of Fig. 4. Note that region II is a *trapping region*, meaning that any solution entering there will remain there. Moreover, in holds that the limit as $t \to \infty$ of any solution $(u_1(t), u_2(t))$ of system (11) starting in regions II at $t = t_0$ is E_1^*. Also, every solution starting in either regions I or III will eventually enter in region II, which completes the proof. ∎

Theorem 4 (*Conditional Exclusion*). *Consider system* (11) *and assume that* $c_{ij} > 1$ $i, j = 1, 2$ *and* $c_1 > 0$. *Then, there exists an equilibrium point* E_+^* *that is unstable while the semi-trivial equilibrium points* E_1^* *and* E_2^* *are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through* E_+^*.

Proof. The hypotheses in the Theorem and Descartes's rule imply that Eq. (29) has one or three real roots. The direct calculations show that $f_2(0) > f_1(0)$ and $f_1(1) > f_2(1)$; thus there exists $u_{1-}^* \in [0, 1]$ such that $f_1(u_{1-}^*) = f_2(u_{1-}^*)$. In addition, $\frac{df_2(u_1)}{du_1} = -c_{21} < 0$ implies that f_2 is strictly decreasing. Besides, $\frac{df_1(u_1)}{du_1} = -\frac{c_1}{c_{12}}(3u^2 + 1) + 2\frac{c_1}{c_{12}}u < 0$ for any $u_1 \in (1, \infty)$. Therefore, f_1 is also strictly decreasing in $[1, \infty)$, there exists a solution of Eq. (29) $[1, \infty)$ and the nullclines meet at the fourth quadrant. Arguing as before, it is not difficult to show that the third solution is in $(-\infty, 0)$. Therefore, there exists a unique nontrivial equilibrium point E_+^* in $(0, 1) \times (0, 1)$ (see panel (iii) in Fig. 4). The proof can be completed arguing as in the proof of the previous Theorem 3.

As for the existence of the separatrix, let us recall that the Poincaré–Bendixon's Theorem estates the possible structure of every non-empty compact ω-limit set of an orbit which contains only finitely many fixed points. Being the system a competitive one (*sensu* [22]) precludes the existence of both periodic orbits or homoclinic orbits. Note

that E_+^* is a saddle–node equilibrium point and the nullclines are its stable manifold, one of the branches joining the trivial equilibrium point E_0^* (an unstable focus) and E_+^*. ∎

Theorem 5 (*Either bi-stable Conditional Coexistence or Species 1 Exclusion*). *Consider system* (11) *and assume that* $c_{12} > 1$, $0 < c_{21} < 1$ *and* $c_1 > 0$. *Consider* c_{1-}^* *as defined in* (15) *and the semi-trivial equilibrium points* E_1^* *and* E_2^*. *Then, for any solution with initial values in the positive cone:*

1. *Assume that* $c_1 \in (c_{1-}^*, \infty)$. *Then, there exist two nontrivial equilibrium points* E_+^* *and* E^* *in the positive cone. Besides,* E_1^* *and* E_+^* *are unstable while* E_2^* *and* E^* *are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through* E_+^*.
2. *Assume that* $c_1 \in (0, c_{1-}^*)$. *Then,* E_2^* *is globally asymptotically stable and* E_1^* *is unstable.*

Proof. It follows by using the ideas used in the proofs of Theorem 3 and Theorem 4. ∎

Theorem 6 (*Coexistence*). *Consider system* (11) *and assume that* $0 < c_{ij} < 1$, $i, j = 1, 2$ *(thus, the semi-trivial equilibrium points* E_1^* *and* E_2^* *are unstable) with* $c_1 > 0$. *Then, for any solution with initial values in the positive cone:*

1. *There exist three equilibrium points* E_+^*, E_-^* *and* E^* *in the positive cone if* $c_1 \in (c_{1-}^*, c_{1+}^*)$, *where* $c_{1\pm}^*$ *were defined in* (15). *In such a case, exist a nontrivial equilibrium point* E_+^* *unstable while* E^* *and* E_-^* *are locally asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through* E_+^*.
2. *The equilibrium point* E^* *is globally asymptotically stable if* $c_1 \in (0, c_{1-}^*) \cup (c_{1+}^*, \infty)$.

Proof. It follows by using the ideas used in the proofs of Theorems 3 and 4. ∎

Appendix C

Theorem 7. *Consider system* (9) *along with the symmetry conditions* $c_1 = c_2 \equiv c_\bullet$ *and* $c_{12} = c_{21} \equiv c_{\bullet\bullet}$. *Consider also the following quantities,*

$$c_\pm^* = \frac{c_{\bullet\bullet}^2 + 20c_{\bullet\bullet} - 8 \pm \sqrt{c_{\bullet\bullet}(c_{\bullet\bullet}-8)^3}}{8}$$

$$c_\pm^{**} = \frac{-3c_{\bullet\bullet}^2 + 20c_{\bullet\bullet} - 8 \pm \sqrt{c_{\bullet\bullet}(9c_{\bullet\bullet}-8)(c_{\bullet\bullet}+8)^2}}{8} \tag{31}$$

$$c^{***} = -\frac{13c_{\bullet\bullet}^2 + \sqrt{-c_{\bullet\bullet}(7c_{\bullet\bullet}-8)^3} - 4c_{\bullet\bullet} - 8}{8(c_{\bullet\bullet}-1)}$$

1. *For any* $0 < c_{\bullet\bullet} < \frac{8}{9}$, $\forall c \in \mathbb{R}^+$, $\tilde{E}^*$ *is a global attractor to the positive cone.*
2. *Assume now that* $\frac{8}{9} < c_{\bullet\bullet} < 1$:

    (a) *For any* $0 < c < c_-^{**}$, $\tilde{E}^*$ *is a global attractor to the positive cone.*
    (b) *For any* $c_-^{**} < c < c_+^{**}$, $\tilde{E}^*$ *is a saddle while* $\tilde{E}_3^*$ *and* $\tilde{E}_4^*$ *are asymptotically stable, so that there exists a separatrix passing through* $\tilde{E}^*$ *that defines the basins of attraction of* $\tilde{E}_3^*$ *and* $\tilde{E}_4^*$.
    (c) *For any* $c_+^{**} < c < c^{***}$, $\tilde{E}_5^*$ *and* $\tilde{E}_6^*$ *are saddle points while* $\tilde{E}^*$, $\tilde{E}_3^*$ *and* $\tilde{E}_4^*$ *are asymptotically stable, so that there exists a separatrix passing through* $\tilde{E}_5^*$ *and* $\tilde{E}_6^*$ *that defines the basins of attraction of* $\tilde{E}^*$, $\tilde{E}_3^*$ *and* $\tilde{E}_4^*$. *Besides, for any* $c^{***} < c < \infty$, $\tilde{E}^*$ *is a global attractor to the positive cone.*

3. *Assume now that* $1 < c_{\bullet\bullet} < 8$:

    (a) *For any* $0 < c < c_+^{**}$, $\tilde{E}^*$ *is a saddle while the semi-trivial equilibrium points* E_1^* *and* E_2^* *are asymptotically stable, so that there exists a separatrix passing through* $\tilde{E}^*$ *that defines the basins of attraction of* E_1^* *and* E_2^*.

(b) *For any $c_+^{**} < c < \infty$, $\tilde{E}_3^*$ and $\tilde{E}_4^*$ are saddle points while $\tilde{E}^*$, E_1^* and E_2^* are asymptotically stable, so that there exists a separatrix passing through $\tilde{E}_3^*$ and $\tilde{E}_4^*$ that defines the basins of attraction of $\tilde{E}^*$, E_1^* and E_2^*.*

4. *Assume now that $c_{\bullet\bullet} > 8$:*

    (a) *For any $0 < c < c_-^*$ or $c_+^* < c < c_+^{**}$, $\tilde{E}^*$ is unstable while the semi-trivial equilibrium points E_1^* and E_2^* are asymptotically stable, so that there exists a separatrix passing through $\tilde{E}^*$ that defines the basins of attraction of E_1^* and E_2^*.*

    (b) *For any $c_+^{**} < c$ and $c_+^* < c$, $\tilde{E}_3^*$ and $\tilde{E}_4^*$ are saddle points while $\tilde{E}^*$, E_1^* and E_2^* are asymptotically stable, so that there exists a separatrix passing through $\tilde{E}_3^*$ and $\tilde{E}_4^*$ that defines the basins of attraction of $\tilde{E}^*$, E_1^* and E_2^*.*

    (c) *For any $c_+^{**} < c < c_+^*$, $\tilde{E}_3^*$, $\tilde{E}_4^*$, $\tilde{E}_5^*$, $\tilde{E}_6^*$ are unstable points while $\tilde{E}^*$, E_1^* and E_2^* are asymptotically stable, so that there exists a separatrix passing through $\tilde{E}_3^*$ and $\tilde{E}_4^*$ that defines the basins of attraction of $\tilde{E}^*$, E_1^* and E_2^*.*

    (d) *For any $c_-^* < c < c_+^{**}$, $\tilde{E}^*$, $\tilde{E}_3^*$ and $\tilde{E}_4^*$ are unstable while E_1^* and E_2^* are locally asymptotically stable, so that there exists a separatrix passing through $\tilde{E}^*$, $\tilde{E}_3^*$ and $\tilde{E}_4^*$ that defines the basins of attraction of E_1^* and E_2^*.*

Proof. For the convenience of the reader, let us follow Section 4.1 and recall that the main analysis tool is, again, the Sturm's Theorem applied to the $g(u_1)$ and $h(u_1)$ (defined in (21) and (22)) in the polynomial Eq. (20). We compute the number of change of signs of the Sturm's sequence of polynomial (20) at $u_1 = 0, 1$ by means of the Sturm's sequences of (21) and (22) denoted by $Seq_g = \{g(u_1), g'(u_1), R_1(u_1), R_2(u_1)\}$ and $Seq_h = \{h(u_1), h'(u_1), T_1(u_1), T_2(u_1), T_3(u_1), T_4(u_1), T_5(u_1)\}$. Many of them have constant sign at $u_1 = 0, 1$, but $R_2(u_1)$, $T_4(u_1)$, $T_5(u_1)$ may display different sign at $u_1 = 0, 1$ depending on the value of $c_\bullet$ and $c_{\bullet\bullet}$. Solving the corresponding equations on $c_\bullet$ yield threshold values defined by (31) (that is to say, expression (25), (26) and (27)). Taking into account the threshold values $c_\pm^*$, c^{***}, $c_\pm^{**}$ we get conditions for the existence of one, three or five real roots as summarized in the Table 2.

1. Direct calculations show that $f_1(0) > f_2(0)$, $f_1(1) < f_2(1)$, then $\exists\, u_1^* \in [0, 1]$, such that $f_1(u_1^*) = f_2(u_1^*)$. Note that none of the expressions in (31) are real numbers for $c_{\bullet\bullet} \in (0, \frac{8}{9})$. The stability of the equilibrium point can be proved as in Theorem 4.

2. For any $c_{\bullet\bullet} \in (\frac{8}{9}, 1)$ the discriminant of $c_\pm^{**}$ and c^{***} are positive. Then,

    (a) A non-trivial equilibrium point $\tilde{E}^*$ exists when $c_\bullet \in (0, c_-^{**})$. Its global stability follows from the proof of Theorem 4.

    (b) Non-trivial equilibrium points $\tilde{E}^*$, $\tilde{E}_3^*$ and $\tilde{E}_4^*$ exist for $c \in (c_-^{**}, c_+^{**})$. Its stability can be assessed as in the proof of Theorem 4. In particular, Fig. 6 illustrates that regions II, IV, V, VI and VII are a *trapping regions*, also the equilibrium point $\tilde{E}^*$ is unstable while $\tilde{E}_3^*$ and $\tilde{E}_4^*$ are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through $\tilde{E}^*$. Note that the symmetry in the phase portrait implies that the straight $u_1 = u_2$ is invariant by the flow of system (9), in fact, it is a separatrix for the basins of attraction for remaining non trivial equilibrium points $\tilde{E}_3^*$ and $\tilde{E}_4^*$. Then, $\tilde{E}_3^*$, $\tilde{E}_4^*$ are asymptotically stable.

    (c) Non-trivial equilibrium points $\tilde{E}^*$, $\tilde{E}_3^*$, $\tilde{E}_4^*$, $\tilde{E}_5^*$ and $\tilde{E}_6^*$ exist whenever $c \in (c_+^{**}, c^{***})$. The stability can be derived as in the above proof of 2-(b). The equilibrium point $\tilde{E}_5^*$ and $\tilde{E}_6^*$ are unstable while $\tilde{E}_3^*$, $\tilde{E}^*$ and $\tilde{E}_4^*$ are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through $\tilde{E}_5^*$ and $\tilde{E}_6^*$.

Statements 3 and 4 can be derived as in the proof of statement 2. The existence of the nullclines follow reasoning as in the proof of Theorem 4. ∎

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