



Universidad  
de Alcalá

TESIS DOCTORAL / PHD THESIS

**COMPETITIVE RESPONSE IN INTERFERENCE COMPETITION  
MODELS**

RESPUESTA COMPETITIVA EN MODELOS DE COMPETENCIA POR INTERFERENCIA

**Hamlet H. Castillo Alvino**

**DEPARTMENT OF PHYSICS AND MATHEMATICS**

FACULTY OF SCIENCES

**June 2020**





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**Conformidad de los directores / Advisors' conformity:**

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*"The laws of nature are nothing more than the mathematical thoughts of God."*

Euclides.





## Resumen

Esta tesis se enmarca en el campo de la Ecología matemática. En particular, se utilizan ecuaciones diferenciales ordinarias (EDOs) para describir la dinámica de dos especies que compiten entre sí por interferencia. La competencia entre especies es, junto con el mutualismo/facilitación y las relaciones depredador-presa/parasitismo, una de las formas esenciales de interacción entre especies.

En la Naturaleza, los seres compiten casi en todo momento, bien sea con individuos de su misma especie, bien sea con individuos de otras especies. Los práctica mayoría de modelos matemáticos de competencia de especies modelados con EDOs giran en torno a los trabajos de Lotka [56], Volterra [87] y Gause [32]. En concreto, a partir de los trabajos de Lotka y Volterra se establece que dos especies pueden coexistir cuando la competencia intra especies es más fuerte que la inter especies [69, 94]. Por su parte, el Principio de exclusión competitiva de Gause dicta que dos especies que ocupan el mismo nicho no pueden coexistir [37]. Sin embargo, este marco teorico choca con la realidad, que muestra sin ambages que las especies consiguen coexistir en mucha mayor medida que lo predicho teóricamente [72, 83, 89].

Se han propuesto distintos paradigmas y mecanismos para superar esta contradicción y establecer un nuevo marco teórico. Una alternativa es describir mecanismos que reduzcan la competencia inter especies (ver [94] y las referencias allí citadas). En [2, 55] se proponen distintas extensiones del principio de exclusión competitiva. La Teoría del nicho ecológico [54, 58] explica que dos especies que compiten dentro del mismo nicho ecológico podrían hacer un uso diferente de los distintos tipos de recurso disponible, lo que se traduce en una reducción de la presión por competencia que una especie ejerce sobre la otra. Otros mecanismos propuestos son, por ejemplo, la dispersión espacial y la heterogeneidad de los hábitats [3, 63, 70], la resolución a la que cada especie percibe los recursos [83], los llamados mecanismos de igualación (tendencia a minimizar en promedio las diferencias en la salud (fitness) de cada especie) y estabilización (tendencia a incrementar la competencia intra especies en relación a la competencia inter especies) [24], mecanismos basados en parásitos específicos de ciertos hospedadores [15, 38, 92] o la estructura por la edad y la distancia entre colonias [11], por citar algunas.

Las explicaciones expuestas se centran bien en estrategias adoptadas por cada especie o bien en condiciones ambientales que las propician. Un enfoque alternativo consiste en describir de manera más detallada cómo interactúan las especies en competencia. Modelizar un fenómeno implica seleccionar las variables esenciales para describirlo y las relaciones relevantes entre las mismas. Existe una tensión evidente entre el nivel de detalle que tiene el modelo y lo manejable que resulta. Los primeros modelos siempre surgen de hacer hipótesis simplicadoras, y el modelo

clásico de competencia de Lotka y Volterra no es una excepción. En concreto, asume implícitamente [72, 94] que

1. Las interacciones entre especies son instantáneas, en el sentido de que el efecto *per capita* sobre un grupo de competidores es el mismo *independientemente* de cuántos sean.
2. Que la tasa de crecimiento per cápita de una especie disminuye linealmente conforme aumenta el tamaño de la otra población.
3. Los individuos están bien mezclados. Por tanto, cualquier individuo de una especie puede interactuar con cualquier individuo de la otra.

Estas hipótesis son totalmente válidas en una primera aproximación, pero distan mucho de ser universales. Sin embargo, comparado los modelos depredador presa, la tarea de refinar el modelo base para darle mayor verosimilitud está poco desarrollada en el caso de la competencia por interferencia. Este hecho contrasta con el gran desarrollo de los modelos de depredador presa, adaptables a la competencia por explotación de recursos (cuya dinámica aparece explícitamente en el modelo).

A pesar de esa falta de desarrollo analítico sistemático, por ejemplo, [7, 85] encontraron evidencias empíricas de que los efectos de la competencia pueden ser denso-dependientes. Esto implica que las nulclinas, las líneas de crecimiento cero de cada población en el plano de fases pueden ser curvas y no sólo rectas (lineales) como en el modelo clásico de Lotka y Volterra. De hecho, en [72] se argumenta que es más interesante obtener información sobre la curvatura de dichas nulclinas que mejorar la precisión con que se estiman experimentalmente los coeficientes de competencia inter especies. Este autor propone un modelo general formulado en términos de la llamada función de disponibilidad de recursos, y demuestra que la curvatura de tales funciones determina la curvatura de la correspondiente nulclina. En el caso de los modelos de depredador-presa se han incorporan modificaciones al modelo clásico en el término de interacción entre especies [12, 25, 28, 40, 77]. En el caso de la competencia entre especies se ajusta experimentalmente la forma de las nulclinas [7, 85] (y referencias que citan estos trabajos), pero no se traduce en un estudio analítico de las propiedades dinámicas del modelo de ecuaciones diferenciales subyacente. Sí se justifica la forma de la curva en términos de "encuentros con los recursos" [74], disponibilidad de recursos [33] o mecanismos de facilitación-competición [94]. Excepciones en este sentido son [1] y [64], que presentan modelos en los que se incorpora la estructura social de las especies, en la que una de ellas forma un rebaño mientras que la otra es más individualista.

En esta tesis se buscan nuevas formulaciones del modelo clásico aplicables a aquellas situaciones en las que no se cumple alguna de las hipótesis arriba expuestas. En concreto, se proponen y analizan los tres modelos que se describen en los siguientes párrafos.

### **Modelo 1. Respuesta competitiva Holling tipo II: tiempo de interacción entre especies.**

La hipótesis fundamental de este capítulo es que los individuos invierten (o consumen) tiempo en el proceso de competencia con la otra especie; es decir, este proceso no es instantáneo. La idea de fondo es la misma que usó Holling en sus trabajos [39, 40], pero adaptada al contexto de la competencia entre especies. Desde otro punto de vista, *fijado* el número de individuos de la especie  $j$ , su influencia sobre la especie  $i$  debería disminuir si el tamaño de la especie  $i$  aumenta.

Los resultados obtenidos indican que, efectivamente, esta respuesta competitiva hace que la presión entre especies sea inferior a la que estipula el modelo clásico. Recuérdese que la posibilidad de coexistencia depende esencialmente de los pesos de la competencia inter e intra especies (según cómo se formule el modelo, moduladas por las tasas de crecimiento). Así, esta nueva formulación permite que haya más situaciones en las que las especies coexisten. Esto sucede a través de los escenarios de bi-estabilidad condicional a favor de la especie  $i$  (en función del número inicial de individuos de cada especie, o bien coexisten, o bien la especie  $i$  elimina a la  $j$ ) y tri-estabilidad condicional (dependiendo de las condiciones iniciales, o bien coexisten, o cualquiera de las dos especies puede eliminar a la otra). En concreto, al analizar los resultados de la competencia en función del tiempo que se invierte en la misma se derivan condiciones para que se de uno u otro escenario en términos de los coeficientes del sistema en el caso de que sólo una especie consume tiempo (de forma significativa) en la competencia. Esta aproximación también es posible en el caso de que las dos especies exhiban esta propiedad, se estudian analíticamente los casos de competencia simétrica y asimétrica, En el caso general se obtiene la información de interés mediante experimentos numéricos.

### **Modelo 2. Respuesta competitiva Holling tipo IV: estrategia de defensa grupal.**

En este capítulo se implementa en el modelo de competencia entre especies el mecanismo de defensa grupal, que ya ha sido descrito en modelos depredador-presa. En concreto, se supone que el tiempo dedicado por la especie  $j$  a competir con la especie  $i$  aumenta linealmente con el tamaño de la especie  $i$ . El gráfico del término que se incorpora al sistema de ecuaciones diferenciales se interpreta también como que para un tamaño fijo de la población  $j$ , el efecto de la competencia sobre la especie  $i$  aumenta cada vez más despacio hasta que, a partir de cierto valor umbral (en el que se alcanza el valor crítico en el que empieza a operar la defensa en grupo) este efecto empieza a disminuir.

Como en el modelo anterior, esta suposición implica que la competencia entre especies es menor (incluso menor que el caso Holling tipo II), lo que parece sugerir que mejoran las expectativas de coexistencia, también a través de escenarios de bi y tri-estabilidad. En este caso el interés está en la fortaleza de la defensa grupal, entendido como cuánto aumenta el tiempo dedicado a competir al aumentar el tamaño de la población del competidor. El esquema de obtención de resultados (sólo una especie exhibe defensa grupal, o las dos con competencia simétrica/asimétrica y análisis numérico allí donde no es posible obtener expresiones cerradas razonables) es similar al del primer modelo.

### **Modelo 3. Un modelo para poblaciones sésiles.**

Los seres sésiles son aquellos que no se mueven. La forma en que interaccionan estos seres es claramente diferente a la de aquellos que son móviles. En este capítulo se propone un modelo de competencia específico para ellos. En particular, como los individuos permanecen inmóviles, sólo establecen competencia con aquellos que se encuentran cerca de ellos, en su entorno vital. De nuevo esto relaja el efecto de la competencia con respecto del modelo clásico, pero en este caso se relajan tanto la intra como la inter especies (esta última más, debido a ciertas hipótesis adicionales necesarias). Mejoran las expectativas de coexistencia, también a través de escenarios de bi y tri-estabilidad, aunque a través de mecanismos diferentes de como sucede en los otros dos modelos. El esquema del capítulo es similar a los dos anteriores y, en particular, se estudia la competencia entre una especie sésil y otra que no lo es.

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very thankful,  
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# Notation

$x_i, i = 1, 2$	Amount of individuals of species.
$r_i, i = 1, 2$	Intrinsic growth rate of species.
$a_{ij}$	Intra ( $i = j$ ) and inter Inter ( $i \neq j$ ) species competition $i, j = 1, 2$ .
$K$	Carrying capacity.
$c_{ij}$	Competitive strength, the effect of species $j$ on species $i$ relative to the effect exerted by $j$ to itself.
$E_n$	Equilibrium points of system $n = 1, 2, 3, 4, 5, \dots$
$\frac{x'_i}{x_i}$	Per capita growth rate of species $i$ .
$N_i$	Number of competitors of species $i \neq j$ that become extinct due the interference of a single individual of species $j \neq i$ .
$T, T_{actv}, T_{int}$	Total time, time that individuals are active (searching for/defending resources or territories, matching,...) and interference time.
$u_i, z_i$	Rescale of variable $x_i$ of system.
$\mathbb{R}_+^2 = (0, +\infty) \times (0, \infty)$	The non-negative cone.
$f_i(u_i), f_i(z_i), f_i(z_i)$	The nullclines associated with the flow of system.
$c_i$	Coefficient rate of the capability of enduring competitors and the intra-species competition rate $a_{ii}$ .
$g_i$	group competitive strength coefficient.
$\psi_{c_1}(c_{12}), \psi_{b_1}(a_{12})$	Unimodal function $\psi$ with fixed $c_1, b_1$ parameter.
$J(u_1, u_2), JF(x_1, x_2)$	Jacobian matrix of dynamical system.
$P(u_i), P_{sw}(w), P_c(z_i)$	Polynomials of the intersections of the nullclines of dynamical system.
$c, \hat{c}$	interference coefficient factor and inter-species competition coefficient under symmetric competition.
$\sqrt{S}$	Vital square interaction space on non-mobile living being individuals species.

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$$-da_{ij}\sqrt{x_i}\sqrt{x_j}$$

Inter-species interactions on the boundary of each species domain.

$$b_i$$

proportion between the local boundary and the perimeter occupied by the entire population.

$$b_i a_{ii} x_i \sqrt{x_i}$$

Inter-species interactions on the boundary of each of them.

$$\text{tr}(J(E_3^\pm), \det(J(E_1)))$$

Trace and determinant of Jacobian matrix.

$$\lambda_n, n = 1, 2$$

Eigenvalues of Jacobian matrix.

$$R_i(z_i) = -\mathbf{rem}(P_c(z_i), P'(z_i))$$

remainder of the euclidean divisions.

$$Seq_c(u_i), Seq_c(z_i)$$

Sturm's sequence of equation  $P(u_i)$  or  $P_c(z_i)$ .

# Scientific diffusion

Throughout this thesis the following original publications in international journals, international congress, and workshop have been produced:

## Internationals journals publication and under review

- H. Castillo-Alvino, M. Marva, *The competition model with Holling type II competitive response to interfering time.*, Journal of Biological Dynamics, (2020). <https://doi.org/10.1080/17513758.2020.1742392> JCR impact factor of 1.70 ( $Q_2, T_2$ ).
- H. Castillo-Alvino, M. Marva, *Interference competition on group defense with Holling type IV competitive response.* Submitted.
- H. Castillo-Alvino, M. Marva, E. Venturino *Modeling interference competition on sessile populations.* Submitted.

## International conferences

- H. Castillo-Alvino, M. Marva, *Interference competition on group defense with Holling type IV competitive response.*, 11th International conference Systems Applied to Biology and Natural Science, DSABNS Feb-2020, Trento, Italy. **(Contributed talk)**
- H. Castillo-Alvino, M. Marva, *The competition model with Holling type II competitive response to interfering time.*, Second Conference Bringing Young Mathematicians Together, BYMAT May-2019, Madrid Spain. **(Poster)**
- H. Castillo-Alvino, M. Marva, *The competition model with Holling type II competitive response to interfering time.*, 10th International conference Systems Applied to Biology and Natural Science, DSABNS Feb-2019, Naples, Italy. **(Poster)**

## Special Workshop

- Special Workshop of the students of P. D. Ciencias, *presentations of progress about the investigations carried out in the academic period 2018-2019, Interference competition on group defense with Holling type IV competitive response.* (U.I Mathematics and Physics), December 2019. **(Contributed talk)**
- Special Workshop of the students of P. D. Ciencias, *presentations of progress about the investigations carried out in the academic period 2017-2018, The competition model with Holling type II competitive response to interfering time.* (U.I Mathematics and Physics), December 2018. **(Contributed talk)**

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# Introduction

This dissertation can be framed in the field of Mathematical Ecology. Ecology is a branch of Biology that is concerned with the interactions between organisms and the environment they are inhabiting. Thus, Mathematical Ecology, one of the many approaches to Ecology, consists of the application of mathematics to describe the above mentioned interactions. In particular, we apply ordinary differential equations (ODE) to describe species interactions and to test ecological hypotheses. ODE are an important modeling tool not only in Ecology, but also in Biology, Physics, Chemistry, Economy, Environmental sciences, Epidemiology or Sociology, to cite few of them.

Roughly speaking, there are three main categories of species interactions: mutualism (interacting is beneficial to both species), competition (the interaction is detrimental for both species) and predator-prey/parasitism (interaction is detrimental for one of the species and beneficial for the other one). The fundamental interaction that we deal with is that of competition between species. Specifically, we will focus on the description through ODE of the long-term behavior (extinction, persistence, coexistence, . . .) of species that interact with each other.

## 1.1 Species competition

Species competition is among the most important biotic factors; living beings compete almost everywhere with individuals of the same species (intra-species competition) and/or individuals of a different species (inter-species competition). There are at three main forms of competition between species [38, 52, 69]:

- In the so-called *exploitation competition* species interact indirectly as they actually compete for a common resource (food, territories). Therefore, the resource for which they compete appears explicitly in the equations as one more state variable. In some sense, this kind of competition resembles two predators (the competing species) feeding on a common prey (the resource).
- A different approach is that of *interference competition*. In this class of models the resource is implicit and the competition happens straight between individuals.

## 1. Introduction

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- Finally, *apparent competition* happens indirectly between two species that are both preyed upon by the same predator. As its name points out, there is no real competition.

The early theory of competition spinned around the works of Lotka [56], Volterra [87] and Gause [32]. Namely, from the Lotka and Volterra works it follows that coexistence is possible when intra-species dynamics is stronger than inter-species dynamics. The Competitive exclusion principle set by Gause stated that two species occupying the same niche can not coexist [37]. This theoretical framework is at odds with reality, given that species coexist much more often than expected within this framework [72, 83, 89].

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 [94] and references quoted there). In [2, 55] extensions of the competitive exclusion principle were proposed. The classical niche theory [54, 58] 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, 63, 70], the resolution at which resources are perceived by each competing species [83], 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) [24], host-specific pets-based mechanism [15, 38, 92] or age-structure and distance between colonies [11].

The above mentioned mechanisms focus on species strategies or environmental constrains. An alternative approach consists on focusing on actual way competition takes place. Modeling a phenomenon entails selecting the relevant variables and capture the key relations between these variables. Therefore, there is tension between the detail level and getting handle able models. Many times the line between both opposite sides is too narrow. Usually, first attempts to model a phenomenon make as many simplifying assumptions as possible. Subsequent versions incorporate gradually more and more details until reaching a given complexity level, that makes model too complicated to get new relevant information from it. For instance, let us have a look at the seminal works of Malthus [60]. In Malthus work constant growth rate was assumed. Many populations growth data follow a Malthusian law in the short term. However, this is a non realistic assumption in the long term, since no ecosystem can provide as many supplies as needed regardless of the total population size. Next, we review the underlying assumptions of the Nootka-Volterra model [56, 87].

### 1.2 Departure model and main assumptions

We focus on interference competition, and the Lotka-Volterra model is given by system

$$\begin{cases} x'_1 = r_1 x_1 - a_{11} x_1^2 - a_{12} x_1 x_2, \\ x'_2 = r_2 x_2 - a_{22} x_2^2 - a_{21} x_1 x_2, \end{cases} \quad (1.1)$$

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  $a_i > 0$  account for intro ( $i = j$ ) and inter ( $i \neq j$ ) species competition, for  $i, j = 1, 2$ . In the absence of species  $j$ , species  $i$  follows a logistic growth law. We will refer to this model as the *classical model*, that is the departure point of this research work. We adopt the *emergent carrying capacities* formulation [16, 43, 76] rather

than using explicit carrying capacities [69, 94]. As noted in [45] writing the logistic equation as  $x' = Rx(1 - x/K)$  exhibits properties that are biologically unrealistic, among them [45] "when the equation is employed in the Voltmeter's competition model, a familiar but incredible conclusion is derived which says that the outcome of competition is entirely independent of the reproductive potential  $r$  of each species".

System (1.1) can be rewritten in the more convenient form

$$\begin{cases} u_1' = r_1 u_1 (1 - u_1 - c_{12} u_2), \\ u_2' = r_2 u_2 (1 - u_2 - c_{21} u_1), \end{cases} \quad (1.2)$$

by defining  $u_i = a_{ii} x_i / r_i$  and the so-called *competitive strength*

$$c_i := \frac{a_{ij} / r_i}{a_j / r_j} \quad (1.3)$$

that gathers intro and inter species competition along with their intrinsic growth rates. The ratio  $a_i / r_i$  measures how large is the effect exerted by species  $j$  on species  $i$  relative to the intrinsic growth rate of species  $i$ . For species  $j$ , the ratio  $a_j / r_j$  measures how large is the effect of intro species competition relative to its intrinsic growth rate. Thus, the competitive strength measures somehow the effect of species  $j$  on species  $i$  relative to the effect exerted by  $j$  to itself.

Competitive strengths rule the competitive outcome of system (1.2), that is equivalent to system (1.1). In words, species  $i$  will survive if the pressure species  $j$  exercises on species  $i$  is lower than the pressure exercised by species  $j$  on itself. That is to say, species  $j$  can not drive species  $i$  to extinction if the competitive strength  $c_i, i \neq j$ , of species  $j$  on species  $i$  is less than 1 (see figure 1.1 for a graphical summary). Namely,

**Theorem 1.1.** *Consider system (1.2). Then, for any solution with initial values in the positive cone*

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

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

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

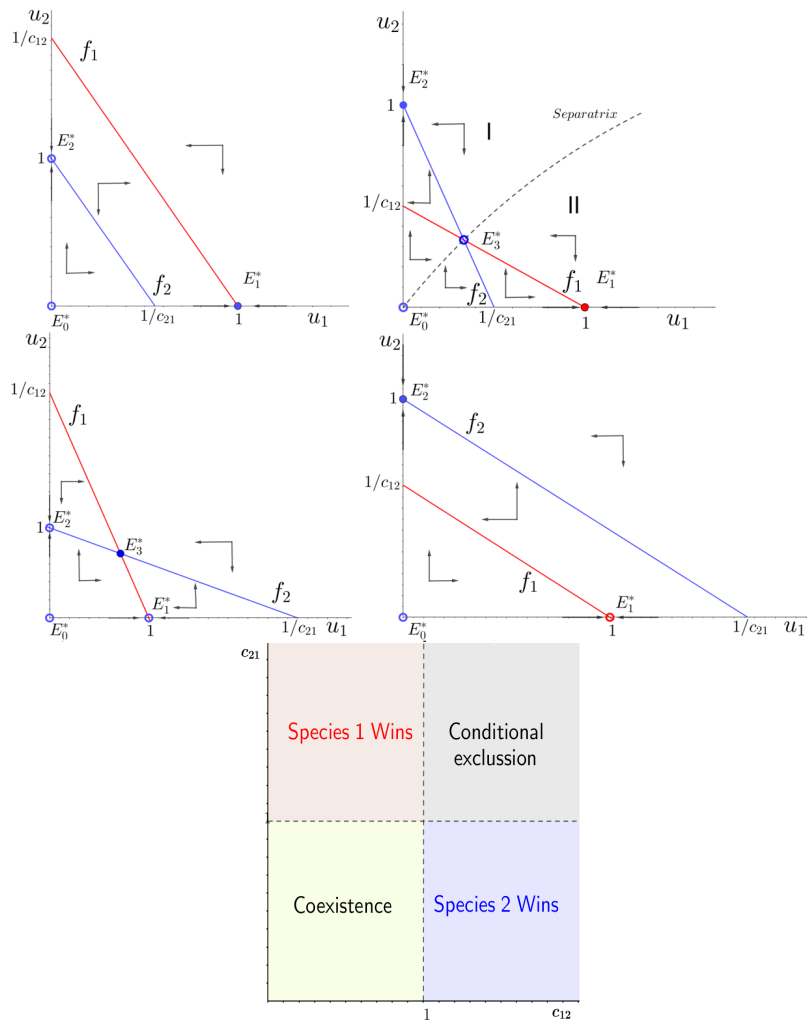
4. *Else  $E_3^*$  exists and is unstable if  $c_{12} > 1$  and  $c_{21} > 1$ . In such a case,  $E_1^*$  and  $E_2^*$  are asymptotically stable, each of which has a basin of attraction defined by a separatist passing through  $E_3^*$ .*

*Proof.* See section 3.5 in [69]. ■

□

Despite of its importance, the classical Lotka-Volterra model was somehow oversimplifying (see section 1.3 for details). For instance, it is assumed that the *per capita* effect of one species on the other is linear to the population size of its competitor. However [7, 85] empirically showed that competitive effects can be density-dependent which entails that the inclines, the zero growth curves of the corresponding differential or difference equations system, are non-linear in contrast to the linear inclines of the classical Lotka-Volterra competition model, although

# 1. Introduction



**Figure 1.1:** Top panel: possible phase portraits of the classical competition system (1.2). Bottom panel: species competition outcomes as function of the competitive strength  $c_{12}$  and  $c_{21}$ .



they did not modified the classical model and mathematically analyzed it. Subsequently, Tunney [72] argued that it is more interesting to focus on the inclines curvature rather than on an 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 inclines There are also works justifying the form of the species interference term based on “food encounters” [74] or on available resources [33] or on a cooperation-competition mechanism [94] but, again, lack of a systematic mathematical analysis. An exception is that of [1] and [64] 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 behavior, so that interactions among the two populations occur mainly through the perimeter of the herd.

In contrast, predator-prey models have been deeply mathematically treated. The term *functional response* was originally coined by [78] as the number of prey actually hunted per predator as a function of prey density. The functional response describes how the population of predators benefits as the size varies. This allows incorporating into the equations characteristic of certain species that are observed empirically.

Rolling [39, 40] described three main types of functional responses, named after Rolling type I, II and III. The base model of Lotka-Volterra follows a functional response of Rolling type I [39]. It is assumed that fixed a number of predators, its effect on prey population is proportional to the number of prey. It is fine as a first approximation, but it is unrealistic since the number of prey that each predator can deal with is usually limited. The functional responses of Rolling types II and III solve this situation [40]. In Rolling type II the interaction term is such that the proportion of prey eaten decreases monotonically as prey density increases. Regarding type III, the interaction term has a Zsigmondy form, so that the proportion of the prey that are consumed is positively density-dependent over some regions of prey density. Subsequently, many alternatives have been proposed to better model other situations. For instance, sometimes the dams have developed group defense tactics Rolling type IV [31, 42, 82, 93].

Currently there is a wide range (more than twenty) of different functional responses, always related to predator-prey models [68, 73, 77]. In addition, [1, 6, 10, 46] recently suggested a “*square root*”, a type functional response focused on predatory species of herd prey, particularly for the herding of large mammals. Their argument is based on the idea that predators can only attack those prey along the perimeter of a herd. The same thoughts (but with different equations) can be found in [46].

Roughly speaking, in this dissertation we enhance the classical competition model with functional response like terms to cover features not included in the base competition model.

### 1.3 Objectives and organization of the thesis

Essentially, this dissertation presents three different modifications of the classical competition model. These modifications look for improve the simplifying assumptions made in the classical interference competition model. In particular:

1. Interacting takes no time. We mean that the *per capital* effect of competition on a group of competitors is the same regardless of its size.

## 1. Introduction

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2. The *per capital* competition effect increases linearly as the population sizes increase regardless of each population size.
3. Individuals are well mixed, so that each individual of one of the species can interact with any other individual of the same/other species.

Challenging these assumptions inspires the chapters of this dissertation, meaning that the corresponding model has been set up to answer the question: “what if this or that simplification does not hold?” Two of the new models consist of a modification of the species interaction term that we name after *competitive response* because of its resemblance with functional response terms in predator prey models. The third model is an adaptation and extension of a predator prey model for structured populations. Full details on the settings, context and results can be found, of course, in the corresponding chapter.

The dissertation is organized as follows: the introductory part of the dissertation consists of the proper Introduction along with lists of tables, figures, notation and an account of the scientific diffusion of the results achieved. The body of the document consists of chapters 2, 3 and 4, where we derive, analyze and discuss each of the above mentioned mechanisms. An sketch of the main assumptions, the aims and the results related to each model can be found at the beginning of each chapter (2, 3, 4). Finally, at chapter 5, we establish global conclusions by discussing together the results achieved for each model.

In the sequel we sketch each of the main chapters (2, 3 and 4).

### Chapter 2: taking into account the interacting time.

The main assumption in this chapter is that competing takes time rather than being instantaneous. For instance, two individuals engaged with each other can not interfere with another one until they complete their contest. This feature was behind the pioneer works of Holling [39, 40] derived in the context of predator-prey models. Such a mechanism, even plausible, has not been implemented on interference competition models. The resulting interaction term admits also a phenomenological interpretation: given a fixed species  $j$  population size, its effect on population  $i$  should decrease as species  $i$  population size increases (because of “lack of time”).

The hypothesis to test is that accounting for the time spent competing should improve the chances of coexisting, since the *actual* pressure of one of the species over the other one is lower than if interactions were instantaneous. Indeed, we have found positive answer to this question.

The classical model is a particular case of the (new) Holling type II competition model. Apart from the competitive outcomes allowed by the classical model, species can coexist via bi conditional coexistence in favor of species  $i$  and tri conditional coexistence scenarios. In the former, both a coexistence equilibrium and the species  $i$  semi-trivial equilibrium point are (locally) asymptotically stable. In the later a coexistence equilibrium and both semi-trivial equilibrium points are (locally) asymptotically stable. In both cases the final outcome depends on the initial amount of individuals of each species. These new dynamical scenarios arise in the regions of the  $c_{12}c_{21}$  parameter space (see the bottom panel of figure 1.1) where the classical competition model predicts either one species exclusion or competitive exclusion due to priority effects.

### Chapter 3: taking into account group defense strategies.

In this chapter we assume that not only interfering is time consumption but also that the larger is the other population size, the more time it takes to population  $j$  compete. This mechanism, known as group defense or Holling type IV functional response [31], has been previously addressed for predator-prey models but not analyzed in the context of interference competition models. Indeed, given a fixed amount of individuals of species  $j$ , the competition rate increases slower as species  $i$  population size  $X_I$  increases. There exists a threshold value for species  $i$  population size such that the effect of  $j$  on  $i$  decreases as  $x_i$  crosses this threshold value, that "fully activates" group defense.

As before, the hypothesis to test is that accounting for the time spent competing should improve the chances of coexisting, since the *actual* pressure of one of the species over the other one is lower as the population size increases. The answer is positive and similar results to those got in Chapter 2 are achieved.

### Chapter 4: Interference competition in sessile populations.

In this chapter we set up a competition model for motionless populations. We assume that individuals are not well mixed; on the contrary, populations are homogeneously grouped and inter-species competition takes place in a boundary layer. Also, as individuals can not move, each of them interacts with few conspecifics that are the closet neighbors.

As a result, both intra and inter species competition effect are lower than for mobile individuals populations. Therefore, we expect that coexistence is more likely than in the classical model. This model is different from the other two, since the classical competition model is not a particular case. Indeed, global coexistence or unconditional one species exclusion is not allowed by the sessile populations competition model. Instead, species coexist (if so) only via tri-stable conditional coexistence.



# Interference competition model with Holling type II interacting response to interfering time

In this chapter <sup>1</sup> we revisit the classical type interaction competition model assuming that individuals invest time in interacting (competing) with individuals of the other species. First, 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:

1. Enlarging the range of parameter values that allow coexistence scenarios and
2. Displaying dynamical scenarios not allowed by the classical model: namely, bi-stable conditional coexistence in favor 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.

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<sup>1</sup>This chapter has been already published [20]

## 2.1 Introduction

The departure assumption in this chapter is that interacting takes time rather than being instantaneous. In other words, two individuals of different species that compete for a given resource do need to invest a certain amount of time to get this resource. The model presented herein extends the classical interference competition model [32] (see also [5]) that becomes the particular case when competition is assumed to be instantaneous. The mechanism is essentially that used in Holling works [39, 40]. Indeed, the interference term of the model takes the form of a Holling type II term [40] 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. However, we have found also competition outcomes not allowed by the classical model. In the so-called *bi-stable conditional coexistence (in favor 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. Also, we have found also benefit interaction, i.e., mutualism outcome allowed results where the species that interact with each other always coexist.

This chapter is organized as follow: in section 2.2 we derive the above mentioned model. We also analyze there those scenarios that are the same as in the classical competition model. In section 2.3 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 2.4 we consider the complete model with competitive response on both species. The system can be analytically analyzed under the assumptions of either symmetric (section 2.4.1) or asymmetric (section 2.4.2) competition. These results are completed in Section 2.4.3 with numerical simulations on the most general model. Finally, section 2.5 is devoted to the discussion of results and to drawn conclusions.

## 2.2 The Holling type II competition model.

The departure model is the classical Lotka-Volterra interaction type model (1.1)

$$\begin{cases} x_1' = r_1 x_1 - a_{11} x_1^2 - a_{12} x_1 x_2 \\ x_2' = r_2 x_2 - a_{22} x_2^2 - a_{21} x_1 x_2 \end{cases} \quad (2.1)$$

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  $i, j = 1, 2$ .

A key assumption in the classical model (2.1) 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 [39, 40] to the current context. As in [40], 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

$$N_i = aT_{actv}x_i$$

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,  $T = T_{actv}$ ; otherwise  $T > T_{actv}$ . Let  $T_{int}$  be the average time that interference takes, so that  $T_{actv} = T - T_{int}N_i$ , that implies

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

that is equivalent to

$$N_i = \frac{aTx_i}{1 + aT_{int}x_i} \quad (2.2)$$

that we call *Holling type II competitive response to interference time*. Plugging this expression in system (2.1) and relabeling coefficients yields

$$\frac{x_i'}{x_i} = r_i - a_{ii}x_i - \frac{a_{ij}x_j}{1 + a_i x_i}, \quad i \neq j, \quad i, j = 1, 2 \quad (2.3)$$

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 behavioral 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 (2.3). et us first rewrite system (2.3) in a suitable way (as we did with system (1.1) to get system (1.2)) by setting  $u_i = a_{ii}x_i/r_i$ ,  $c_i = a_i/a_{ii}$  and the so-called *competitive strength* (1.3) defined in section 1.2 given by

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

so that (2.3) becomes

$$\begin{cases} u_1' = r_1 \left( u_1 - u_1^2 - \frac{c_{12}u_1u_2}{1 + c_1u_1} \right) \\ u_2' = r_2 \left( u_2 - u_2^2 - \frac{c_{21}u_2u_1}{1 + c_2u_2} \right) \end{cases} \quad (2.4)$$

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Note that  $c_i$  is the ratio of the capability of endure competitors (meaning that the larger is  $a_i$ , the more time needs a competitor to make species  $i$  surrender) and the intra-species competition rate  $a_{ii}$ . Let us recall that the outcomes of the classical competition model can be found in Theorem 1.1.

We next show that system (2.4) is well behaved, in the sense of the following theorem:

**Theorem 2.1.** *Consider system (2.4). 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.  $\square$

The following result establishes the existence and stability properties of the so-called trivial and semi-trivial equilibrium points of system (2.4), that is the same as in the classical model. From now on, we assume that  $r_i > 0$  for  $i = 1, 2$ .

**Theorem 2.2.** *Consider system (2.4). 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 calculation. The stability conditions follow from an standard analysis of the eigenvalues of the Jacobian matrix.  $\square$

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.

### 2.3 Interference competition model with 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

$$\begin{cases} u_1' = r_1 \left( u_1 - u_1^2 - \frac{c_{12} u_1 u_2}{1 + c_1 u_1} \right) \\ u_2' = r_2 (u_2 - u_2^2 - c_{21} u_1 u_2) \end{cases} \quad (2.5)$$

System (3.5) is a particular case of system (2.4), so that we already know that it is well behaved. Proposition 2.2 also holds in relation to the existence and local stability of the trivial and semi-trivial equilibrium points.



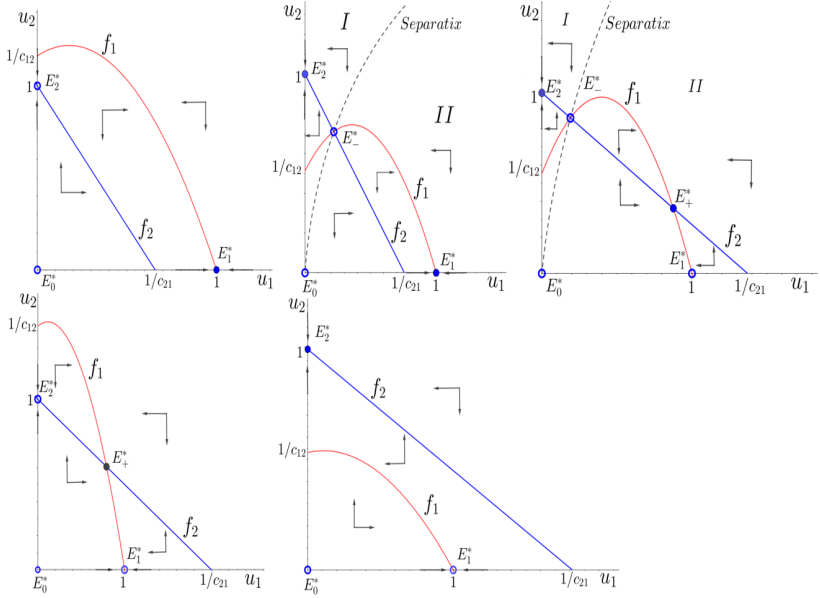


Figure 2.1: Possible phase portrait of system (3.5).

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 (3.5), see figure 2.1 and note that panel (v) leads to a dynamical scenario that is not covered by the classical system (see figure 1.1).

Indeed, figure 2.1 suggest that most of the outcomes (4 over 5) of system (3.5) are qualitatively the same as in the classical model. The following result displays conditions that describe those scenarios.

**Theorem 2.3.** *Consider system (3.5). 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,

$$(1 - c_1 - c_{12}c_{21})^2 < 4c_1(c_{12} - 1). \quad (2.6)$$

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

$$E_+^* = (u_{1+}^*, u_{2+}^*) \quad (2.7)$$

where

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

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and

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

that is globally asymptotically stable to the positive cone.

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

$$E_-^* = (u_{1-}^*, u_{2-}^*) \quad (2.8)$$

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, and  $E_1^*$  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 2.1(v)) and ii) the case of tangent nullclines in the first quadrant (see Figure 2.2).

*Proof.* Consider the nullclines associated to the flow of system (3.5) 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 2.1) 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

$$c_1u_1^2 + (1 - c_1 - c_{12}c_{21})u_1 + c_{12} - 1 = 0 \quad (2.9)$$

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 (2.6) holds (that is equivalent to the discriminant of the solution of equation (2.9) being negative and nullclines do not meet). However condition (2.6) 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 [5] yields the global stability of  $E_1^*$ .

Regarding statement (2), we have already said that condition (2.6) is equivalent to the discriminant of the solution of equation (2.9) 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, [5] or [69].

□

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 (2.9) and solving the resulting equation on  $c_{21}$ , plays a key role.

**Lemma 2.1.** *Consider the function*

$$\psi_{c_1}(c_{12}) := \frac{1 - c_1 + 2\sqrt{c_1(c_{12} - 1)}}{c_{12}}, \quad c_{12} \geq 1 \quad (2.10)$$

then,  $\psi_{c_1}$  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 favor of species 1*. Otherwise, species 2 wins always.

**Theorem 2.4.** *Consider system (3.5) 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 (3.5) in the positive cone if, and only if,*

$$0 < \frac{c_1 + c_{12}c_{21} - 1}{2c_1} < 1 \quad (2.11)$$

*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  $\partial R_i$  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 (2.11) holds. In such a case, the equilibrium point  $E_-^*$  (defined in (2.8)) is unstable while  $E_2^*$  and  $E_+^*$  (defined in (2.7)) 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  $0 < \frac{1 + c_1 - c_{12}c_{21}}{2c_1} < 1$  fails, no positive equilibrium exists.*

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*Proof.* Let us recall that the non-trivial equilibrium points  $E_{\pm}^* = (u_{1\pm}^*, u_{2\pm}^*)$  are the solutions to equation (2.9) 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 (2.10).

1. Condition  $c_{21} < \psi_{c_1}(c_{12})$  with  $1 < c_{12} < \infty$  is equivalent to equation (2.9) to have complex roots, so that there are no non-trivial equilibrium points. Analyzing the flow on the phase portrait as in [5] 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 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 (3.5) at  $E^*$ . Namely, consider the Jacobian matrix of system (3.5) at any  $(u_1, u_2) \in \mathbb{R}^2$

$$J(u_1, u_2) = \begin{pmatrix} r_1 - 2r_1u_1 - r_1 \frac{c_{12}u_2}{(1+c_1u_1)^2} & -r_1 \frac{c_{12}u_2}{1+c_1u_1} \\ -r_2c_{21}u_2 & r_2(1-2u_2-c_{21}u_1) \end{pmatrix} \quad (2.12)$$

At an equilibrium point  $(u_1^*, u_2^*)$  of system (3.5) 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 (2.12) at the equilibrium point  $(u_1^*, u_2^*)$  becomes

$$J(u_1^*, u_2^*) = \begin{pmatrix} r_1 - 2r_1u_1^* - r_1 \frac{1-u_1^*}{1+c_1u_1^*} & -r_1 \frac{c_{12}u_2^*}{1+c_1u_1^*} \\ -r_2c_{21}u_2^* & -r_2u_2^* \end{pmatrix} \quad (2.13)$$

Zero is an eigenvalue of matrix (2.13) if, and only if,  $|J(u_1^*, u_2^*)| = 0$ . Direct calculation lead to

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

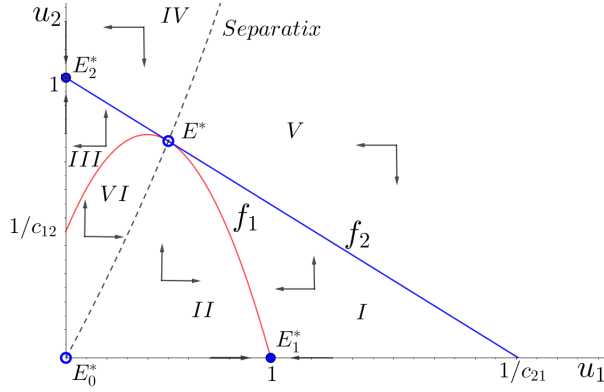
so that

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

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

Besides, consider the corresponding phase portrait (see figure 2.2). A first claim is that regions I and III are trapping regions, meaning that any solution entering one of them can not 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  $E_2$ .

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  $u_1 > 1$ .



**Figure 2.2:** Phase portrait related to 2b. Solid points denote the locally asymptotically stable equilibrium points  $E_1^*$  and  $E_2^*$  while the equilibrium  $E^*$  is non stable.

Note that  $c_{21} > \psi_{c_1}(c_{12})$ ,  $c_{12} > 1$  along with condition (2.11) imply that  $0 < u_{1\pm}^*$ . Besides,  $u_{1+}^* < 1$  is equivalent to

$$\sqrt{(c_1 + c_{12}c_{21} - 1)^2 - 4c_1(c_{12} - 1)} < c_1 + 1 - c_{12}c_{21} \quad (2.14)$$

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 (2.14) and rearranging terms we get that (2.14) 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, 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  $E_+^* = E^* = E_-^*$ .

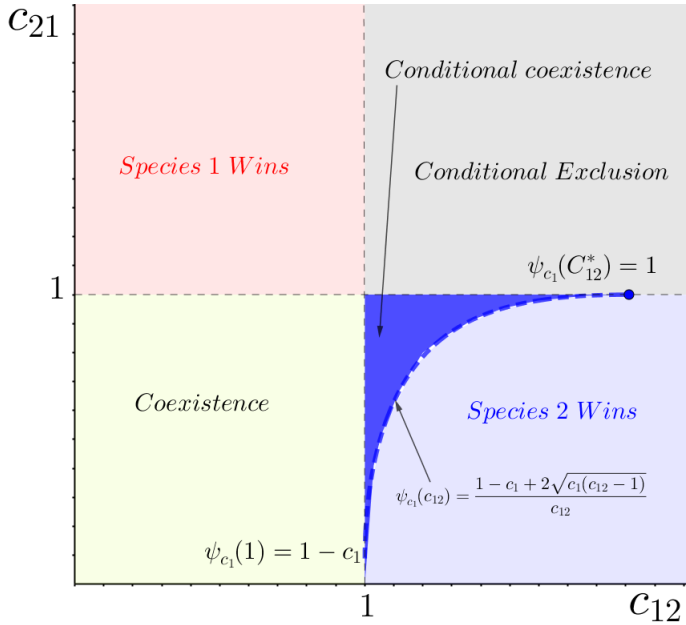
4. Note that  $f_1(0) = 1/c_{12}$ ,  $f_2(0) = 1$  and  $f_1(1) = 0$ ,  $f_2(1) = 1 - c_{21}$ . Thus,  $f_2(0) > f_1(0)$  and  $f_2(1) > f_1(1)$ , so that no positive equilibrium points exist.
5. It follows from the previous discussion. □

With this we finish the analysis of system (3.5). The above results are deeply discussed in section 2.5.

## 2.4 Interference competition model with Holling type II response on both species.

We turn now our attention to the complete model (2.4). Section 3.3 suggests that we must expect either settings such that the classic competition model and system (2.4) behave qualitatively the

## 2. Interference competition model with Holling type II interacting response to interfering time



**Figure 2.3:** Competition outcomes of system (3.5) as function of the competitive strengths  $c_{12}$ ,  $c_{21}$ .

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 2.3, we focus on the existence and stability of the non-trivial equilibrium points. The nullclines of system (2.4) are parabolas, defined by

$$\begin{aligned} u_2 &= f_1(u_1) = (1 - u_1)(1 + c_1 u_1)/c_{12}, \\ u_1 &= f_2(u_2) = (1 - u_2)(1 + c_2 u_2)/c_{21} \end{aligned} \quad (2.15)$$

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

$$P(u_1) = \gamma_4 u_1^4 + \gamma_3 u_1^3 + \gamma_2 u_1^2 + \gamma_1 u_1 + \gamma_0 = 0 \quad (2.16)$$

where

$$\begin{aligned} \gamma_4 &= -c_1^2 c_2 \\ \gamma_3 &= 2c_1 c_2 (c_1 - 1) \\ \gamma_2 &= 2c_1 c_2 - c_1 (c_2 - 1) c_{12} - c_2 (c_1 - 1)^2 \\ \gamma_1 &= (c_1 - 1)(c_2 - 1) c_{12} - 2(c_1 - 1) c_2 - c_{12}^2 c_{21} \\ \gamma_0 &= (c_2 + c_{12})(c_{12} - 1) \end{aligned} \quad (2.17)$$

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 (2.4). However, there are two ecologically meaningful scenarios, symmetric and asymmetric competition [95], that lead to simplifications in (2.17) that allow an analytic study that we address next.

### 2.4.1 Symmetric competition and Holling type II competitive response.

Symmetric competition takes place, for instance, between individuals of different species with similar phenotypic traits [95]. This idea can be translated to system (2.4) by setting the model coefficients as

$$c_1 = c_2 \equiv c, \quad c_{12} = c_{21} \equiv \hat{c} \quad (2.18)$$

see [47]. In such a case, coefficients (2.17) specialize into

$$\begin{aligned} \gamma_4 &= -c^3 \\ \gamma_3 &= 2c^2(c-1) \\ \gamma_2 &= 2c^2 - c(c-1)\hat{c} - c(c-1)^2 \\ \gamma_1 &= \hat{c}(c-1)^2 - 2(c-1)c - \hat{c}^3 \\ \gamma_0 &= (c+\hat{c})(\hat{c}-1) \end{aligned} \quad (2.19)$$

It turns out that  $c = 1$  and  $\hat{c} = 1$  are candidate to be threshold values for the behavior 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 2.2.** *Consider the nullcline curves (2.15) with coefficients (2.18), 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)  $f_2(f_1) = u_1, \forall u_1 \in \left[ \frac{c-1}{2c}, \infty \right)$ .
- (b)  $f_1(f_2) = u_1, \forall u_1 \in \left( -\infty, \frac{(c+1)^2}{4c\hat{c}} \right]$ .

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

$$u_{1\pm}^{**} = \frac{c - \hat{c} - 1 \pm \sqrt{(c - \hat{c} - 1)^2 + 4c}}{2c} \quad (2.20)$$

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

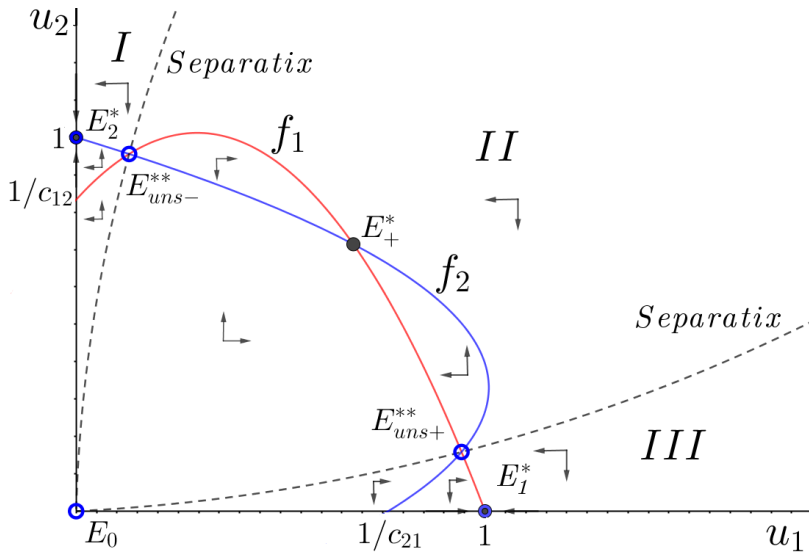
*Proof.* It follows from direct calculations. □

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 2.4).

**Theorem 2.5.** *Consider system (2.4) 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 (2.20) 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,

## 2. Interference competition model with Holling type II interacting response to interfering time



**Figure 2.4:** Phase portrait in the symmetric competition scenario that displays the tri-stability conditional coexistence outcome.

- (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

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

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

$$u_{1uns\pm}^{**} = \frac{c + \hat{c} - 1 \pm \sqrt{(c + \hat{c} - 1)^2 - 4(\hat{c}^2 + (c - 1)\hat{c} - c)}}{2c} \quad (2.21)$$

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

*Proof.* Let us recall that system (2.4) possesses, at most, four equilibrium points and lemma 2.2 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 (2.15), 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



## 2.4 Interference competition model with Holling type II response on both species.

all the solutions are bounded, as stated in proposition 2.1. The case  $\hat{c} = 1$  follows from the previous discussion.

2. Dividing  $P(u_1)$ , the polynomial (2.16) with coefficients (2.19), 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 (2.21). Therefore, whether  $u_{1uns\pm}^{**}$  is real or complex depends on the discriminant of the right hand side of equation (2.21). Equating to zero the discriminant of (2.21) is equivalent to

$$c = c_{\pm}^* := \hat{c} - 1 \pm 2\sqrt{\hat{c}(\hat{c} - 1)} \quad (2.22)$$

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

- (a) For any  $0 < c < c_+^*$  it follows that  $u_{uns\pm}^{**} \in \mathbb{C}$ . 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 (2.4) 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 [48]).
- (b) Direct calculations show that  $u_{1+}^* = u_{1+}^{**} = u_{1-}^{**}$  at  $c = c_+^*$ . Thus, two branches of equilibrium points  $E_{uns+}^{**}$  and  $E_{uns-}^{**}$  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 [48] 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. □

### 2.4.2 Asymmetric competition and Holling type II competitive response.

Asymmetric competition [51] takes place, for instance, between individuals of different species with dissimilar phenotypic traits [95]. 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 (2.17) become

$$\begin{aligned} \gamma_4 &= -c \\ \gamma_3 &= 2(c - 1) \\ \gamma_2 &= 2 - (1 - c)\hat{c} - (c - 1)^2/c \\ \gamma_1 &= \hat{c} - (c - 1)(1/c - 1)\hat{c} - 2(c - 1)/c \\ \gamma_0 &= (1/c + \hat{c})(\hat{c} - 1) \end{aligned} \quad (2.23)$$

## 2. Interference competition model with Holling type II interacting response to interfering time

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As before,  $c = 1$  and  $\hat{c} = 1$  are candidates to be a threshold value for the qualitative behavior of the solutions of system (2.4).

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

**Theorem 2.6.** *Consider system (2.4) 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 theorems 2.1 and 2.5. □

### 2.4.3 The general case: numerical analysis.

As we have already said, the equilibrium points of system (2.4) are the roots of the 4th degree polynomial equation (2.16). These solutions depend on the coefficients (2.17) that depend on  $c_i$  and  $c_{ij}$ , that is, on four parameters. Closed expressions exist for the roots of (2.16), 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 the algorithm written in MatLab software. From the results found in sections 3.3, 2.4.1 and 2.4.2 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 2.3.

As there are no analytical results for the complete model different from those already obtained at the beginning of section 4.2, we left the results of the numerical experiments to the discussion and conclusions section 2.5.

## 2.5 Discussion and conclusions.

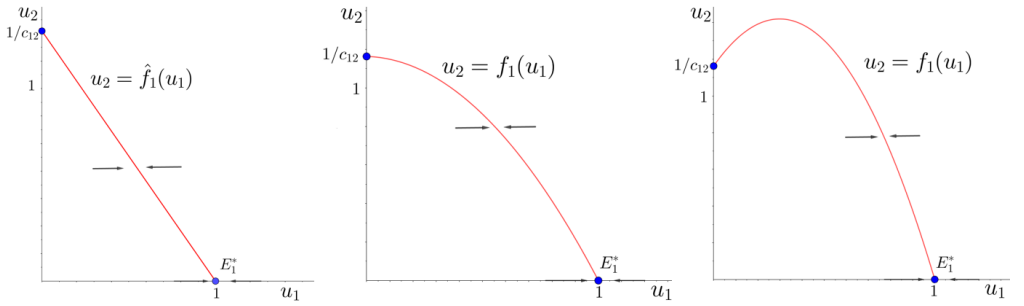
In this chapter we have revisited the classical competition model (2.1) under the assumption that interfering with competitors of other species takes time. We have found that i) the classical competition model is a particular case of the model derived herein when interactions do not consume

time, ii) the more time interfering with competitions takes the more likely coexistence is and, indeed, iii) the new model allows multi-stability escenarios.

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 [72, 94] 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 2.5) and in system (2.4) ( $u_2 = f_1(u_1)$ , central and right panels in figure 2.5), where

$$u_2 = \hat{f}_1(u_1) := \frac{1}{c_{12}}(1 - u_1) \quad u_2 = f_1(u_1) := \frac{1}{c_{12}}(-c_1 u_1^2 + (c_1 - 1)u_1 + 1) \quad (2.24)$$

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.



**Figure 2.5:** The nullcline  $u_1' = 0$  of system (2.4) for increasing values of  $c_1$ : left,  $c_1 = 0$  (i.e., the classical Lotka-Volterra model (2.1)), center,  $c_1 \in (0, 1)$  and right,  $c_1 > 1$ .

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 (2.4), 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,

- Condition  $0 < c_1 < 1$  implies that  $\tilde{u}_1 < 0$  and the nullcline defined by  $f_1$  in (2.24) is decreasing for  $u_1 \geq 0$  (see central panel in figure 2.5). The behavior 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 (2.15) is in the first quadrant (right panel in figure 2.5). As a consequence, if  $0 < u_1 < \tilde{u}_1$  species 1 keeps growing even if  $u_2$  increases moderately (but remaining 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

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growths and crosses the threshold value  $\hat{u}_1$  this trend is reversed (although things are still better for them than 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 2.1). However, for large enough values of  $c_1$  the nullclines switch their position giving rise to a bi-stable conditional coexistence in favor of species 2 scenario (as in the top right panel in figure 2.1)

According to [83, 94] the common interpretation of the early theory of competition [32, 56, 87] 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 behavioral point of view, the above discussion suggests that resist to species 2 may be beneficial to species 1 [62, 67] (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 (2.10) (see lemma 2.1) plays a key role.

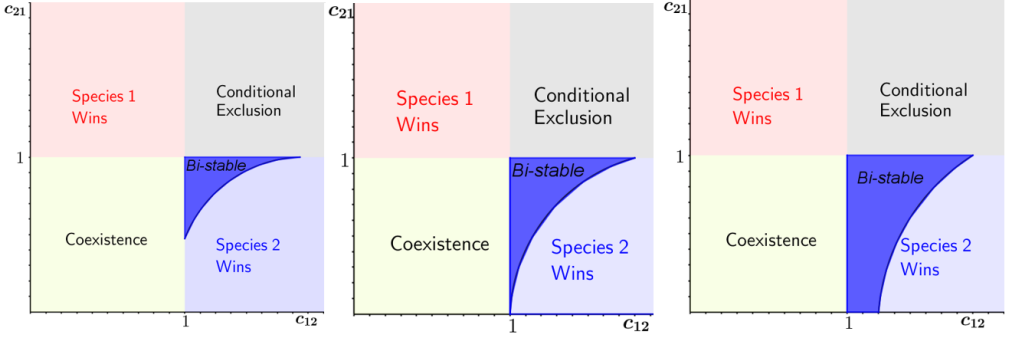
Let us assume that  $0 < c_{21} < 1$  and  $1 < c_{12}$ , that corresponds to the (unconditional) species 1 exclusion in the classical model. Proposition 2.4 tells us that both species can coexist via bi-stable conditional coexistence if

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

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  $\psi_{c_1}$  (see figure 2.3), 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 behavior of the model in case of strong competition ( $1 < c_{21}$  and  $1 < c_{12}$ ) and the new region in the



**Figure 2.6:** Competition outcomes of system (3.5) as function of the competitive strengths  $c_{12}$ ,  $c_{21}$  for increasing values of  $c_1$  (from left to right). The code color is the same as in figure 1.1 except the dark blue region that represents bi-stable conditional coexistence region in favor 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 code is available in [19]) and has been edited to improve it. . Parameter values are  $0 < c_{12}, c_{21} < 2$ ,  $c_2 = 0$  and, from left to right  $c_1 = 0.3, 1, 1.8$

$c_{12}c_{21}$  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.

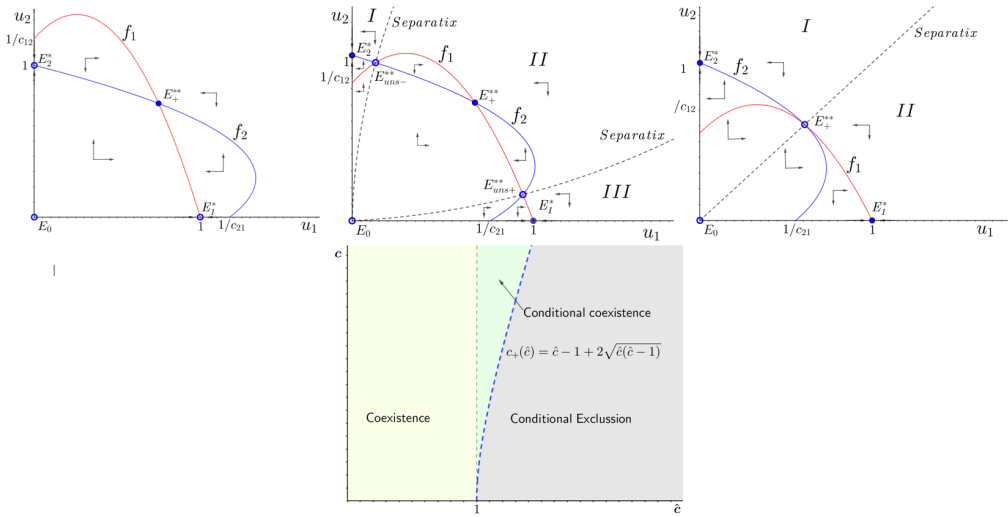
We have first analyzed the symmetric and asymmetric competition scenarios, that have its own applied interest and for which we have achieved analytical results with close expressions for equilibrium and threshold values.

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 2.7.

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 on the initial number of individuals of each species species either will coexist or one of them will go extinct. This result is straight against the classical thoughts [32, 56, 87], 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 favor of the lower competitor if the upper competitor expands large enough time taking resources. (see proposition 2.6). Again, this result is at odds with classical results [32, 56, 87] and illustrates the importance of looking carefully at how interactions take place.

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**Figure 2.7:** Competition outcomes of system (2.4) 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  $0 < c < \hat{c} - 1 + 2\sqrt{\hat{c}(\hat{c} - 1)}$ ).

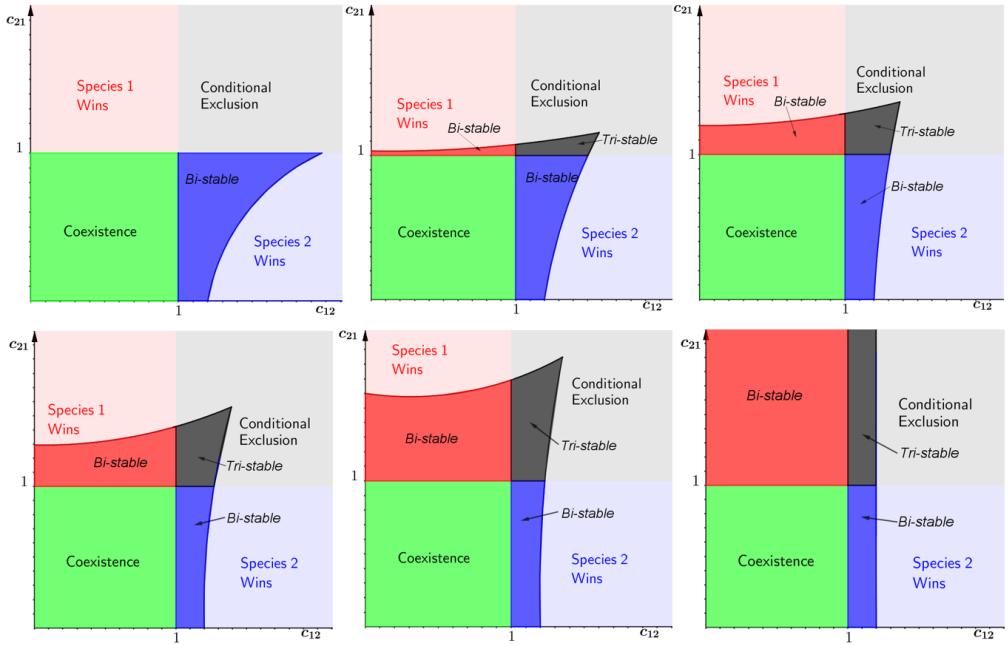
Finally, we examine via numerical results the competition outcomes for the complete system (2.4), that are not qualitatively different from the dynamical scenarios already shown. The source code used can be found in [19].

We have found that  $c_i > 0$  for  $i = 1, 2$  yield the existence of bi-stable conditional coexistence regions in favor of each species (see the dark red and dark blue regions in figure 2.8). 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 (2.10), 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 subregion. The classical model (2.1) predicts conditional exclusion due to priority effects in this region. Instead, model (2.4) allows species to coexist, again, provided that competitive abilities, initial values and competing time are well balanced, see figure 2.8.

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 2.8). As previously mentioned, a bi-stable coexistence region in favor of species 2 appears as  $c_2$  becomes larges than 0. Besides, the bi-stable coexistence region in favor of species 1 is reduced as  $c_2$  increases (see the panels in figure 2.8). Finally, numerical experiments suggest that the bi-stable coexistence region in favor of species 1 converges to a vertical strip as  $c_2 \rightarrow \infty$  (see bottom left panel in figure 2.8).

Interestingly, both bi and tri-stable conditional coexistence have been also found in the context of competition models on patchy environments with individual dispersal [63] or eco-



**Figure 2.8:** Competition outcomes of system (2.4) 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 color is the same as in figure 1.1 except the dark blue region that represents bi-stable conditional coexistence region in favor of species 1, dark-red region stands for bi-stable conditional coexistence region in favor of species 2 and the dark-gray region refers for the tri-stable conditional coexistence region. The figure is based on numerical calculations (the code is available in [19]) 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  $c_2 = 0, 1.15, 1.65, 1.9, 6, 100000$

epidemic competition models [15].





# Interference competition on group defense with Holling type IV competitive response

In this chapter<sup>1</sup> we investigate the role of group defense in the context of species interference competition. We rederive a model that extend the classical interference competition model [32] (see also [5]) by incorporating a Holling type IV term [40], [49] that we call *Holling type IV competitive response on group defense*. In our framework the competition model takes into account the increase on the time spent to snatch resources to other species' individuals due to group defense strategy (of the other species). It can be seen as a continuation of our previous work [20] described in the chapter 2, where the so called Holling type II competitive response was introduced in the classical interference competition model to incorporate the time spent in interfering with competitors. The resulting model expands the outcomes allowed by the classical Lotka-Volterra competition model by,

1. Enlarging the range of parameter values that allow coexistence scenarios.
2. Displaying dynamical scenarios not allowed by the classical model in the form of multi-stable scenarios: bi/tri-stable conditional coexistence (species can either coexist or one/any of them go extinct), bi/tri-stable unconditional coexistence (there exist two or three possible coexistence steady states).

Our results lighten the balance between intra/inter species competitive pressure that is behind competing species coexistence that starting from the outcomes [72], [94]. Besides, the model presented herein displays stable alternative states in which the species coexist unconditionally as a result of the group defense strategy. This mechanism is an alternative explanation to empirical observations [36].

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<sup>1</sup>The content of this chapter has been submitted to a journal and it is under review [20]

## 3.1 Introduction.

Species competition is a key driver for communities dynamics. Species compete for resources, mating, territories, etc. . . . Ecologists consider to main kinds of competition: exploitative competition or interference competition, depending on whether resources dynamics are explicit or not in the underlying model [72], [34].

Species competition is present under many different forms and strategies including aggressiveness [9], [29]. In particular, group defense has been observed among these mechanisms [66] [50] for both vertebrate or invertebrate animals. For example, the ant species *Aphaenogaster cockerelli* and *Pogonomyrmex barbatus* compete for seed resources in the Chihuahuan desert and 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 [11] (see also [88]). Experimental studies [80] shows the reasons why the Humpback whales *Megaptera novaeangliae* interferes with the attack of the killer whales *Orcinus orca* when they hunt their food.

Group defense is well described in the context of predator prey models, being the first one [31]. This mechanism usually modelizes predators intake rate as an one humped (concave) function that depends on the number of prey. That means that at low densities, the predators intake increases as the number of prey increases. That is, the more prey, the more likely is catching them. However, once population prey achieves a critical size, there are enough individuals to face predators and, thus, defend themselves. Therefore, predators intake subsequently decreases as the number of predators increases beyond this threshold value. This feature takes the general form of

$$\frac{mx}{a_0 + a_1x + a_2x^2}$$

and it is usually called Holling type IV functional response in order to complete the “catalogue” of Holling type functional responses I, II and III [40], [27] (but see also [44], [31], [93]). Note that this functional form was first introduced in the context of microbiology [4] and was named after Monod-Haldane functional responses.

There exist many derivations of functional response (always in predator prey models) that take into account the so called *handling time*, i.e., the time spent by the predator handling preys. The usual assumption is that the handling time is linearly increasing with respect to  $N$  (the total amount of preys). There are variations of this idea, as in [22], where the functional response is derived by assuming both a linearly increasing handling time and an inverse-linear attack rate. Other authors proposed a simplified Monod-Haldane functional response that include inhibitory effects [42] that resemble group defense.

Recently, the Holling type IV functional response has been proposed to describe the short-term intake rate of dry matter in large mammalian in interference competition [65], although the authors do not use differential equations.

This work is aimed to derive in a consistent way and analyze a competition model that takes into account the time spent of a group defense with individuals of another species. This model will extend the classical interference competition model [32] (see also [5]) by incorporating a Holling type IV term [40] that we call Holling type IV competitive response on group

defense. It can be seen as a continuation of our previous work [20], where the so called *Holling type II competitive response* was introduced in the classical interference competition model to incorporate the time spent in interfering with competitors.

We have found (when considering group defense) that there exist range of parameter values that lead to competition outcomes different from those allowed by the classical model. Firstly, in the so called *bi-stable conditional coexistence (in favor of the species  $i$ ) scenario* either species coexist or species  $i \neq j$  goes extinct, depending on the initial number of individuals (i.e. due to priority effects). Secondly, the *tri-stable conditional coexistence scenario* allowed either species coexistence or any of them to go extinct due to priority effects. We have found also a *bi-stable and tri-stable unconditional coexistence scenario*, meaning that group defense enables species coexistence in either 2 or 3 alternative steady states. From a mathematical point of view, it means the existence of 3 or 3 positive asymptotically stable equilibrium points. This finding supports the empirical observation that coexistence is much more frequent than what the classical competition model predicts (see [20] for a discussion).

This work is organized as follow: in section 2 we derive the above mentioned model. In section 3 we assume that just one of the species displays group defense. Section 4 is devoted to the full model. We first analyze the case of symmetric competition and then numerically approach the most general case. Finally, section 5 is devoted to the discussion of results and to drawn conclusions. Part of the mathematical results have been sent to the appendix section 6.

## 3.2 The Holling type IV competition model.

The departure model is the classical Lotka-Volterra competition model

$$\begin{cases} x'_1 = r_1 x_1 - a_{11} x_1^2 - a_{12} x_1 x_2 \\ x'_2 = r_2 x_2 - a_{22} x_2^2 - a_{21} x_1 x_2 \end{cases} \quad (3.1)$$

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  $i, j = 1, 2$ .

The *per capita growth rate* of the classical model (3.1) decrease linearly with  $x_i$  and  $x_j$  ( $i \neq j$ ), i.e.,

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

Let recall that the assumption of pressure of a fixed number of individuals of species  $j$  on species  $i$  is the same *regardless* the amount of individuals of species  $i$ , would not makes sense *in reality*. This assumption is not always true in interference competition, since a fixed number of the species,  $j$  cannot compete in the same way on the species  $i$  when there is a group defense, i.e., a group (20 or 5000) of the species  $i$  that compete with the species  $j$  by resource take time.

We present an alternative formulation that, essentially, is an adaptation of [49] to the current context. The first part of the exposition follows [20]: as in [40], 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  $j \neq i$  is given by

$$N_i = aT_{actv} x_i$$

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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,  $T = T_{actv}$ ; otherwise  $T > T_{actv}$ . Let  $T_{int}$  be the average time that interference takes, so that  $T_{actv} = T - T_{int}N_i$ , that implies

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

that is equivalent to

$$N_i = \frac{aTx_i}{1 + aT_{int}x_i} \quad (3.2)$$

that we called *Holling type II competitive response to interference time* in [20].

We assume now that the interference time is not constant; instead, it increases linearly with the number of individuals of species 1

$$T_{int} \equiv (b + dx_i)T_{int}$$

which modelizes group defense; therefore

$$N_i = \frac{aTx_i}{1 + T_{intx}abx_i + T_{intx}adx_i^2},$$

We call Holling type IV *competitive response to interference time on group defense*. Note that either  $b$  or  $d$  equal zero, so that  $d = 0$  means that assembling individuals of species 1 has no effect while  $b = 0$  means that group defense is a common feature in species 1. Plugging this expression in system (4.1) and relabeling coefficients yields

$$\frac{x'_i}{x_i} = r_i - a_{ii}x_i - \frac{a_{ij}x_j}{1 + a_ix_i^2}, \quad i \neq j, \quad i, j = 1, 2, \quad (3.3)$$

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  $x_i^2$  for a fixed amount of individuals of species  $j$ .

The competitive response on group defense defined above can be interpreted as the ability of a group individuals of the species  $i$  to reduce the inter species competition impact when species  $i$  population size becomes larger than species  $j$  population size ( $i \neq j$ ).

Now, we analyze the system (4.1) and compare the competition outcomes to those yield by the classical competition. Let us rewrite system (3.1) provided that  $u_i = a_{ii}x_i/r_i$ , the competitive strength  $c_{ij} = a_{ij}r_j/(r_ia_{ii})$  introduced in (1.3) in section 1.2 and  $g_i = a_i/a_{ii}$ :

$$\begin{cases} u'_1 = r_1 \left( u_1 - u_1^2 - \frac{c_{12}u_1u_2}{1 + g_1u_1^2} \right) \\ u'_2 = r_2 \left( u_2 - u_2^2 - \frac{c_{21}u_2u_1}{1 + g_2u_2^2} \right) \end{cases} \quad (3.4)$$

System (3.1) is a particular case of (3.4) when  $g_i = 0$ . Let us point out that the behavior of the classical competition model has been described in Theorem 1.1 (section 1.2).

Direct calculations show that system (3.4) is well behaved, in the sense of the following theorem 3.1

**Theorem 3.1.** Consider system (3.4). 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 axes, say  $(u_1(t_0), u_2(t_0)) = (u_{01}, 0)$ , 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 direct 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 (3.4). From now on, we assume that  $r_i > 0$  for  $i = 1, 2$ .

**Theorem 3.2.** Consider system (3.4) with  $g_i > 0, i = 1, 2$  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  $c_{ji} > 1, i \neq j$ .
  - (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 calculation. The stability conditions follow from a standard analysis of the eigenvalues of the jacobian matrix. ■

The following sections that are devoted to understand the effect on the competition outcome of considering Holling type IV competition terms (competitive response on group defense).

### 3.3 Holling type IV competitive response on just one species.

In this section, we assume that only species 1 has the capacity to defend themselves as a group when both species compete. Thus, we analyze system

$$\begin{cases} u_1' = r_1 \left( u_1 - u_1^2 - \frac{c_{12}u_1u_2}{1 + g_1u_1^2} \right) \\ u_2' = r_2(u_2 - u_2^2 - c_{21}u_1u_2) \end{cases} \quad (3.5)$$

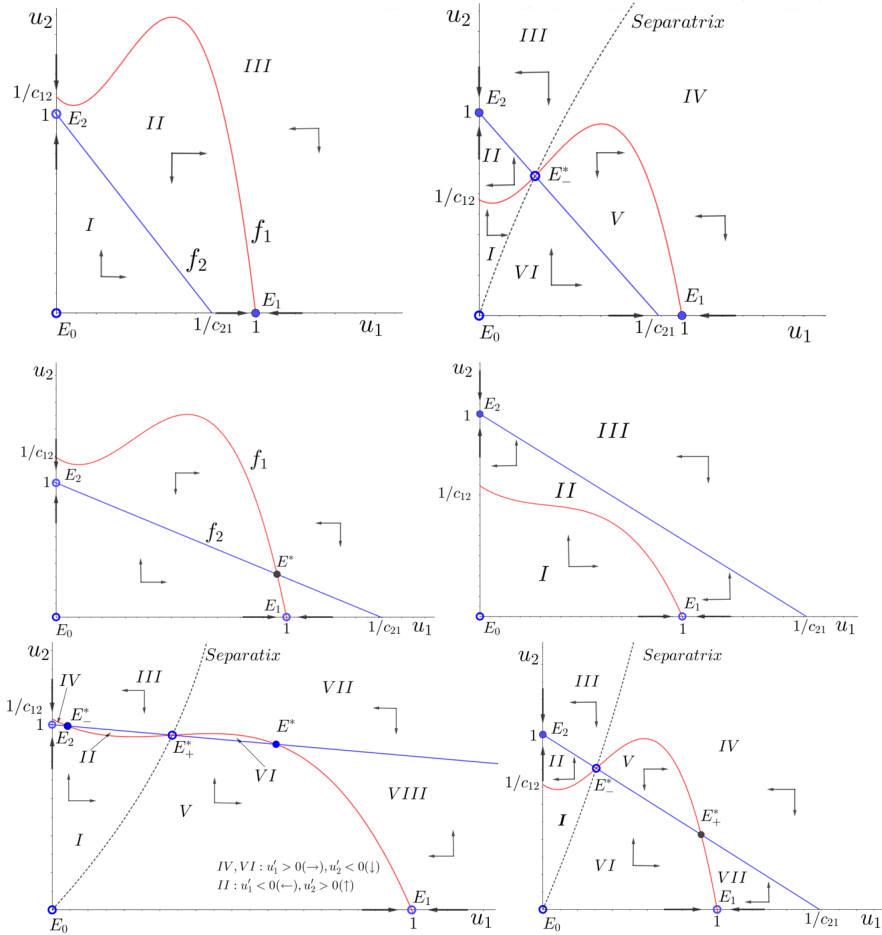
System (3.5) is a particular case of system (3.4), so that we already know that it is well behaved. Theorem 3.2 is fulfilled and states the existence and local stability of the trivial and semi-trivial equilibrium points.

In the sequel, we focus on the nontrivial equilibrium points. Note that the nullcline  $u_2 = f_2(u_1)$  that solves  $u_2' = 0$  is either a straight line, as in the classical model. In contrast, the nullcline  $u_2 = f_1(u_1)$  that solves  $u_1' = 0$  is either  $f_1 \equiv 0$  or a polynomial of third degree. This feature shows the differences between the outcomes of the classical model (3.5) and the current

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model, see figure 3.1 and note that panel (i)' and (iv)', in the blue shadowed rectangle box leads a new dynamic scenario (see figure 4.6).

The following results display conditions that describe those scenarios such that the asymptotic behavior of the solutions of system (3.5) is the same as in system (4.1).



**Figure 3.1:** Possible phase portrait first model with Holling type IV response (3.5).

**Theorem 3.3** (specie 1 wins). *Consider system (3.5) with  $g_1 > 0$ . Then, for any solution with initial values in the positive cone,  $E_1^*$  is globally asymptotically stable if  $c_{21} > 1$  and  $0 < c_{12} < 1$ .*

**Proof:** First consider the nullclines (3.6) of system (3.5),

$$f_1(u_1) = \frac{1}{c_{12}}(-g_1 u_1^3 + g_1 u_1^2 - u_1 + 1), \quad f_2(u_1) = 1 - c_{21} u_1 \quad (3.6)$$

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

$$P(u_1) = u_1^3 - u_1^2 + \frac{s}{g_1}u_1 - \frac{r}{g_1}$$

where,

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

Applying the Sturm's theorem we obtain the Sturm's sequence

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

where first terms are the polynomial of third-degree, the second term  $P'(u_1)$  is the derivative of the polynomial  $P(u_1)$  and the remainder terms  $R_i(u_1), i = 1, 2$ , are the residue of euclidean division of  $R_1(u_1) = rem(P(u_1), P'(u_1))$  and  $R_2(u_1) = rem(P'(u_1), -R_1(u_1))$  multiplying it by -1.  $Seq_p$  display the number of sign variation ( $V(0) - V(1)$ ) of  $P(u_1)$  located in the interval  $u_1 \in [0, 1]$  that shows the number of real roots in this interval. So, analyzing the sign of the term  $R_2(u_1)$  yields the threshold values

$$g_{1\pm}^* = \frac{27r^2 - 18sr - s^2 \pm \sqrt{(r-s)(9r-s)^3}}{8r} \quad (3.7)$$

where

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

that proves the existence of one real roots. So, if the discriminant  $(r-s)(9r-s)^3 < 0$  there exists a real root. Besides, as  $f_1(1) > f_2(1)$  and  $f'_1(u_1) < 0, f'_2(u_1) = -c_{12}f_1(u_1)$  decrease and  $f_2(u_1)$  decrease constantly to  $u_1 \in (0, \infty)$ , then, this real root is in the fourth quadrant.

Figure 3.1-(ii) displays that every solution  $(u_1(t), u_2(t))$  of system (3.5) which starts in regions I at  $t = t_0$  must approach the semi-trivial equilibrium solution  $E_1^*(1, 0)$  as  $t \rightarrow \infty$ . Also, every solution  $(u_1(t), u_2(t))$  of (3.5) which starts in region III at time  $t = t_0$  and remains there  $\forall t \geq t_0$  must also approach the semi-trivial equilibrium solution  $E_1^* = (1, 0)$ . Next, observe that any solution  $(u_1(t), u_2(t))$  of system (3.5) which starts on nullclines  $u_2 = f_1(u_1)$  or  $u_2 = f_2(u_1)$  must immediately afterwards enter region II. Finally, if a solution of the system (3.5) leaves region III, then it must cross the nullclines  $u_2 = f_1(u_1)$  and immediately afterwards enter region II. Therefore, the region II is a *trapping region* and it occurs when the condition  $(r-s)(9r-s)^3 < 0$ , i.e.,  $c_{1\pm}^*$  fails, so the solution approaches the semi-trivial equilibrium solution  $E_1^* = (1, 0)$ . ■

**Theorem 3.4** (conditional exclusion.). *Consider system (3.5) and assume that  $c_{ij} > 1 \quad i, j = 1, 2$  and  $g_1 > 0$ . Then, there exist a equilibrium point  $E_-^*$  that is unstable while  $E_1^*$  and  $E_2^*$  (defined in theorem 3.2) are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through  $E_-^*$ .*

**Proof:** First, let us define  $E_-^*$ . With the above conditions Descartes's rule shows that exist one or three real roots for the polynomial  $P(u_1)$ . The direct calculations show that if  $f_2(0) > f_1(0)$  and  $f_1(1) > f_2(1)$  then  $\exists u_{1-}^* \in [0, 1]$  such that  $f_1(u_{1-}^*) = f_2(u_{1-}^*)$ . For values  $u_1 \in (1, \infty)$  we have  $\frac{df_1(u_1)}{du_1} = -\frac{g_1}{c_{12}}(3u^2 + 1) + 2\frac{g_1}{c_{12}}u < 0$ , so  $f_1$  decreases and  $\frac{df_2(u_1)}{du_1} = -c_{21} < 0$  which implies that  $f_2$  decreases constantly. This show that the second real root is in the fourth quadrant In the same way, we can show that the remain root is in the third quadrant. Figure 3.1-(iii) illustrate this situation. Therefore, exist a nontrivial equilibrium point  $E_-^*$  in the positive cone  $u_1 \in [0, 1]$ .

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We follow the outline as the theorem 3.3. Figure 3.1-(iii) displays that every solution  $(u_1(t), u_2(t))$  of system (3.5) which starts in regions I at  $t = t_0$  must approach the semi-trivial equilibrium solution  $E_2^* = (0, 1)$  as  $t \rightarrow \infty$ . Similarly, every solution  $(u_1(t), u_2(t))$  of (3.5) which starts in region III at time  $t = t_0$  and remains there  $\forall t \geq t_0$  must also approach the semi-trivial equilibrium solution  $E_2^* = (0, 1)$ . Besides, the regions IV, V, VI illustrate the above behavior where the semi-trivial equilibrium solution is  $E_1^* = (1, 0)$  as  $t \rightarrow \infty$ . Next, observe that any solution  $(u_1(t), u_2(t))$  of system (3.5) that starts on nullclines  $u_2 = f_1(u_1)$  or  $u_2 = f_2(u_1)$  must immediately afterwards enter region II or V. Finally, if a solution of the system (3.5) leaves region III or IV, then it must cross the nullclines and immediately afterwards enter region II or V. So, the regions II and V are a *trapping regions* and  $E_1^*$  and  $E_2^*$  are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through  $E_-^*$ . ■

Let's recall that the number of real roots for the polynomial  $P(u_1)$  are given by the conditions of  $c_{1\pm}$  found at analyze of  $R_2(u_1)$ , that ensure the sign variations in the Sturm's sequence  $Seq_p$  which were developed in the above theorem. Next Theorem displays  $c_{1-}$  plays a key rule to prove the existence of the nontrivial equilibrium points.

**Theorem 3.5** (bi-stable conditional coexistence). *consider system (3.5) and assume that  $c_{12} > 1$ ,  $0 < c_{21} < 1$  and  $g_1 > 0$ . Then, for any solution with initial values in the positive cone:*

1. *There exist two nontrivial equilibrium points  $E_+^*$  and  $E_-^*$  in the positive cone if  $g_1 \in (c_{1-}^*, \infty)$ , where  $c_{1-}^*$  was defined in (3.7). In such a case, the nontrivial equilibrium point  $E_-^*$  defined in theorem 3.4 is unstable while the semi-trivial  $E_2^*$  and nontrivial  $E_+^*$  are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through  $E_-^*$ .*
2. *The semi-trivial equilibrium point  $E_2^*$  is globally asymptotically stable if  $g_1 \in (0, c_{1-}^*)$ . In such a case, the semi-trivial equilibrium point  $E_1^*$  is unstable.*

**Proof:** First, consider the nullclines (3.6) of system (3.5), Descartes's rule shows that there exist one or three real roots of the polynomial  $P(u_1)$ . If  $f_1(u_1) = f_2(u_1)$  we obtain the third degree equation

$$P(u_1) = u_1^3 - u_1^2 + \frac{s}{g_1}u_1 - \frac{r}{g_1}, \quad r = 1 - c_{12}, s = 1 - c_{12}c_{21}$$

The conditions and existence of nontrivial equilibrium points can be argued as in theorem 3.3. If  $(r - s)(9r - s)^3 > 0$  there exist two nontrivial equilibrium points  $E_{\pm}^*$  in the interval  $[0, 1]$  when  $g_1 \in (g_{1-}^*, \infty)$ . But, when the discriminant values are less than zero the condition fails, no positive equilibrium exists. The remaining root of the equation lies in the third quadrant and it can be argued in the same way that in the theorem 3.4. Defined the previous, analyzing the phases plane of figure 3.1-(iv)' we proves it the stability of the equilibrium as the following:

1. It follows arguing as in theorem 3.4. This argument shows the local stability at the nontrivial and semi-trivial equilibrium point  $E_2$  and  $E_+^*$ . Figure 3.1-(iv)' illustrates that the regions II, V and VII are a *trapping regions*, also the equilibrium point  $E_-^*$  is 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. The global stability of the semi-trivial equilibrium point  $E_2^*$  can derived as in theorem 3.3. Figure 3.1-(iv) illustrates that region II is a *trapping region* and the solution approaches the semi-trivial equilibrium solution  $E_2^* = (0, 1)$ .



■

**Theorem 3.6** (Coexistence). *Consider system (3.5) and assume that  $0 < c_{ij} < 1$ ,  $i, j = 1, 2$  with  $g_1 > 0$ . 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  $g_1 \in (g_{1-}^*, c_{1+}^*)$ , where  $c_{1\pm}^*$  were defined in (3.7). 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  $g_1 \in (0, c_{1-}^*) \cup (c_{1+}^*, \infty)$ .*

**Proof:** The conditions and existence of non-trivial equilibrium points can be argued as in Theorem 3.5. Again we can observe that  $c_{1\pm}^*$  is fulfilled when the value of the discriminant is positive ( $(r-s)(9r-s)^3 > 0$ ) unconditional coexistence in two nontrivial equilibrium points exist or classical stable scenario exist, but when the value of the discriminant is negative ( $(r-s)(9r-s)^3 < 0$ ), i.e., for values  $c_{21} \in (0, 1), (9 + \frac{8}{c_{12}}, \infty)$ , only  $E^*$  is globally asymptotically stable in the positive cone and the classical stable scenario remains.

The steady state of equilibrium points can be argued as in Theorem 3.4. Figure 3.1-(i') illustrates that the regions II, IV, VI and VII are a *trapping regions*, also the equilibrium point  $E_+^*$  is unstable while  $E^*$  and  $E_-^*$  are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through  $E_+^*$ . Besides, Figure 3.1-(i) illustrates that the regions II and IV are a *trapping regions* and it occurs when the conditions  $g_1 \in (0, g_{1-}^*) \cup (g_{1+}^*, \infty)$  with  $(r-s)(9r-s)^3 > 0$  or  $g_{1\pm}^*$  fails. ■

### 3.4 Holling type IV competitive response on both species.

In this section, we turn our focus to the complete model (3.4). The previous section shows qualitatively similar dynamic scenarios between the classic competition model (4.1) and the system (3.5), and also expand the conditions for coexistence. For Holling type IV competitive response on both species displays a similar panorama of coexistence although a little more complex than the above section.

After theorem 3.3, we seek for the existence and stability of the nontrivial equilibrium points. The nullclines of system (3.4) are polynomial of third degree, defined by

$$u_2 = f_1(u_1) = \frac{1}{c_{12}}(-g_1 u_1^3 + g_1 u_1^2 - u_1 + 1), \quad u_1 = f_2(u_2) = \frac{1}{c_{21}}(-g_2 u_2^3 + g_2 u_2^2 - u_2 + 1) \quad (3.8)$$

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

$$P(u_1) = \frac{1}{c_{12}^3 c_{21}} \sum_{k=0}^9 \gamma_k u_1^k, \quad (3.9)$$

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where

$$\begin{aligned}
 \gamma_9 &= g_1^3 g_2 \\
 \gamma_8 &= -3g_1^3 g_2 \\
 \gamma_7 &= 3g_1^2 g_2 (1 + g_1) \\
 \gamma_6 &= g_1^2 g_2 (c_{12} - g_1 - 9) \\
 \gamma_5 &= g_1 g_2 [g_1 (9 - 2c_{12}) + 3] \\
 \gamma_4 &= g_1 g_2 [g_1 c_{12} - 3g_1 + 2c_{12} - 9] \\
 \gamma_3 &= c_{12} g_1 (c_{12} - 4g_2) + g_2 (9g_1 + 1) \\
 \gamma_2 &= c_{12} [g_2 (1 + 2g_1) - g_1 c_{12}] - 3g_2 (g_1 + 1) \\
 \gamma_1 &= c_{12}^2 (1 - c_{12} c_{21}) + g_2 (3 - 2c_{12}) \\
 \gamma_0 &= (c_{12} - 1)(c_{12}^2 + g_2)
 \end{aligned} \tag{3.10}$$

Unfortunately, this expression is too involved to get any biological insight. However, an ecologically meaningful scenario called symmetric competition [95] describe a biological interpretation reduced (3.10) it allows an analytic study. In addition, we have performed a numerical analysis for both asymmetric competition and the general case that will be explained in the discussions and conclusions section.

#### 3.4.1 Symmetric competition under Holling type IV competitive response.

The symmetric competition takes place between individuals of different species with similar phenotypic traits [95] (see also, [47]). That said, we define the parameters of competitive strength and group defense coefficient as  $c_{12} = c_{21} \equiv \hat{c}$  and  $g_1 = g_2 \equiv g$ . In such a case, equation (3.9) can be written as follow:

$$P(u_1) = \frac{1}{\hat{c}^4} q(u_1) h(u_1), \tag{3.11}$$

where,

$$q(u_1) = cu_1^3 - cu_1^2 + (1 + \hat{c})u_1 - 1$$

and

$$\begin{aligned}
 h(u_1) &= g^3 u_1^6 - 2g^3 u_1^5 + [g^3 + g^2(2 - \hat{c})] u_1^4 \\
 &\quad - 2g^2(2 - \hat{c})u_1^3 + [g^2(2 - \hat{c} + g(\hat{c}^2) - \hat{c} + 1)] u_1^2 \\
 &\quad + (-g\hat{c}^2 + 2g\hat{c} - 2g)u_1 + (g + \hat{c}^2 - g\hat{c} - \hat{c}^3)
 \end{aligned}$$

We have performed a complete analysis of system (3.4) under symmetry conditions in terms of the competitive strength  $\hat{c}$  and the group defense strength coefficient  $c$ . The main analysis tool is the Sturm's theorem applied to factors  $g(u_1)$  and  $h(u_1)$  of the polynomial equation (3.11).

As announced in section 1, we have found parameter values that lead to the same competition outcomes as in the classical model and others that do not. In particular, we refer firstly to the so called bi-stable conditional coexistence (in favor of the species  $i$ ) either species coexist or species  $i \neq j$  goes extinct, depending on the initial number of individuals (i.e. due to priority effects). Secondly, the tri-stable conditional coexistence scenario when either a group of individuals of species  $i$  coexists or any of them go extinct due to priority effects, but also the bi-stable and tri-stable unconditional coexistence scenario when either a group of the species  $i$  coexists until a competitive strength moderate.

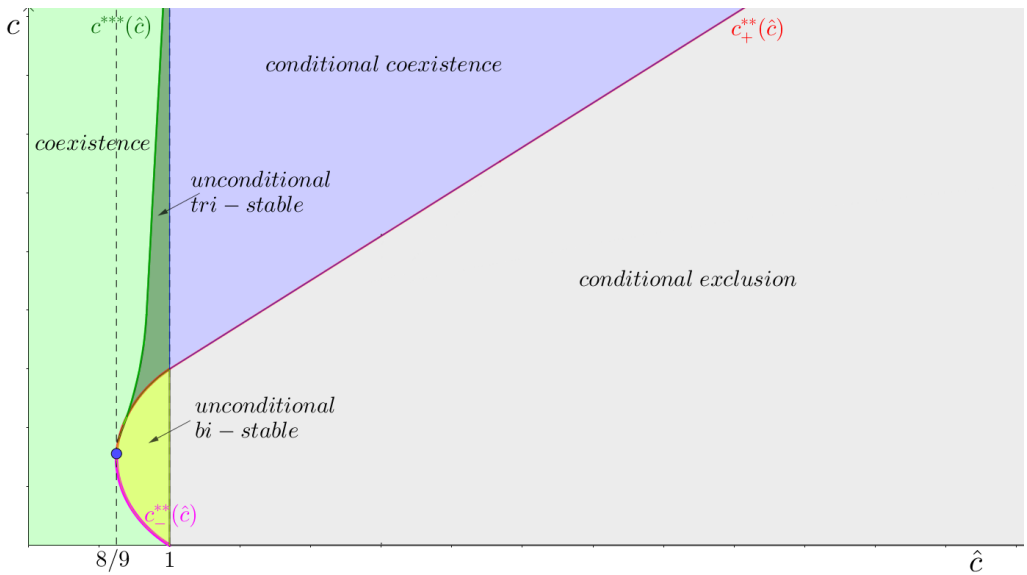
It should be noted that the aforementioned analysis yields scenarios that are different from a mathematical point of view but not different from the species competition outcome perspective. We have summarized the results in table 3.1 and figure 3.2 for the biological approach.

### 3.4 Holling type IV competitive response on both species.

In the sequel we describe in theorems 3.7, 3.8, 3.9 and 3.10 the above mentioned dynamical outcomes, that are summarized in table 3.1 and figure 3.2. The proof of these theorems are gathered in the proof of Theorem 6.1.

Theorem	Competition outcomes	$\hat{c}$ values	$g$ values
3.7	Classical coexistence	$\hat{c} \in (0, 1)$	$g \in (0, c_+^{**})$ $g \in (g^{***}, \infty)$
3.8	Multi-stability	$\hat{c} \in (\frac{8}{9}, 1)$	$g \in (g_+^{**}, g_-^{**})$ $g \in (g_+^*, g^{***})$
3.9	Classical exclusion	$\hat{c} \in (1, \infty)$	$g \in (0, g_+^{**})$
3.10	Conditional coexistence	$\hat{c} \in (1, \infty)$	$g \in (g_+^{**}, \infty)$

**Table 3.1:** Conditions  $\hat{c}$  and  $g$  for the existence of nontrivial equilibrium points of the system (3.4) in the positive cone under the behavior of symmetric competition that correspond for the different biologically competition scenarios.



**Figure 3.2:** Competition outcomes of system (3.4) under symmetric competition as function of the competitive strength  $\hat{c}$  and  $g$ , the ability of a group individuals of species to limit the other species' competitive strength. Code color: green, dark green and yellow represents the global coexistence, bi-stable and tri-stable unconditional coexistence, respectively, while blue and light black represents the conditional coexistence and conditional exclusion regions, respectively.

The following Theorem 3.7 describes conditions on parameters  $g$  and  $\hat{c}$  that yield the classical coexistence scenario with a single positive global attractor.

### 3. Interference competition on group defense with Holling type IV competitive response

**Theorem 3.7** (Classical coexistence). *Consider system (3.4) along with the symmetry conditions  $g_1 = g_2 \equiv g$  and  $c_{12} = c_{21} \equiv \hat{c}$ . Then, there exist a global attractor  $E^*$  to the positive cone if one of the following conditions hold*

1.  $0 < \hat{c} < \frac{8}{9}$  regardless of the value of  $g \in \mathbb{R}^+$ .
2.  $\frac{8}{9} < \hat{c} < 1$  and any  $0 < g < g_-^{**}$ , where

$$g_-^{**} = \frac{-3\hat{c}^2 + 20\hat{c} - 8 - \sqrt{\hat{c}(9\hat{c} - 8)(\hat{c} + 8)^2}}{8} \quad (3.12)$$

is a quantity that springs up from the application of Sturm's Theorem (see the proof of Theorem 6.1, the ideas are the same as in the derivation of  $g_{1\pm}^*$  in (3.7)).

See figure 3.3, panel (i).

**Proof:** See the proof of Theorem 6.1. ■

Next result estates conditions leading to multi-stable coexistence states, that are not allowed by the classical model (4.1).

**Theorem 3.8** (Unconditional multi-stability). *Consider system (3.4) along with the symmetry conditions  $g_1 = g_2 \equiv g$  and  $c_{12} = c_{21} \equiv \hat{c}$  and  $\frac{8}{9} < \hat{c} < 1$ . Then,*

1. For any  $g_-^{**} < g < g_+^{**}$ , where

$$g_+^{**} = \frac{-3\hat{c}^2 + 20\hat{c} - 8 + \sqrt{\hat{c}(9\hat{c} - 8)(\hat{c} + 8)^2}}{8} \quad (3.13)$$

shows up as  $g_-^{**}$  did in Theorem 3.7, there exists  $E^*$  a saddle point and two asymptotically stable equilibrium points  $E_3^*$  and  $E_4^*$ . Besides, the line  $u_1 = u_2$  is separatrix passing through  $E^*$  that defines the basins of attraction of  $E_3^*$  and  $E_4^*$ , that are symmetrically located with respect to the separatrix, as shown in figure 3.3, panel (ii).

2. For any  $g_+^* < g < g^{***}$ , where

$$g_{\pm}^* = \frac{\hat{c}^2 + 20\hat{c} - 8 \pm \sqrt{\hat{c}(\hat{c} - 8)^3}}{8} \quad (3.14)$$

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

show up in a similar context as  $g_-^{**}$  in Theorem 3.7. Then, there exist two saddle points  $E_5^*$  and  $E_6^*$  three asymptotically stable equilibrium points  $E^*$ ,  $E_3^*$  and  $E_4^*$  in the positive cone. There exist separatrices passing through  $E_5^*$  and  $E_6^*$  that define the basins of attraction of  $E^*$ ,  $E_3^*$  and  $E_4^*$ . Note that due to the symmetry of the model  $E^*$  is on the line  $u_1 = u_2$  and that all the other equilibrium points and separatrices are symmetrically arranged with respect to  $u_1 = u_2$ , as shown in figure 3.3, panel (iii).

**Proof:** See the proof of Theorem 6.1. ■

Next result establishes conditions leading to the competitive exclusion of one of the two species due to priority effects.

**Theorem 3.9** (One species exclusion). *Consider system (3.4) along with the symmetry conditions  $g_1 = g_2 \equiv g$  and  $c_{12} = c_{21} \equiv \hat{c}$ . Assume now that  $1 < \hat{c} < \infty$ . Then, for any  $0 < g < g_+^{**}$ , where  $g_+^{**}$  is that from (3.13), there exists a saddle  $E^*$  while the semi-trivial equilibrium points  $E_1$  and  $E_2$  are asymptotically stable, so that  $u_1 = u_2$  a separatrix passing through  $E^*$  that defines the basin of attraction of  $E_1$  and  $E_2$ , as shown in figure 3.3, panels (iv) or (vi).*

**Proof:** See the proof of Theorem 6.1. ■

Finally, next result describes the parameter values that enable conditional coexistence.

**Theorem 3.10** (Conditional coexistence). *Consider system (3.4) along with the symmetry conditions  $g_1 = g_2 \equiv c$  and  $c_{12} = c_{21} \equiv \hat{c}$ . Assume also that  $1 < \hat{c} < \infty$ . Then, for any  $g_+^{**} < g < \infty$ , where  $c_+^*$  is that defined in (3.13), it follows that there exist two saddle points  $E_3^*$  and  $E_4^*$  and three asymptotically stable equilibrium points  $E^*$ ,  $E_1$  and  $E_2$ , as well as separatrices passing through  $E_3^*$  and  $E_4^*$  that defines the basin of attraction of  $E^*$ ,  $E_1$  and  $E_2$ , as shown in figure 3.3, panels (v) or (vii).*

### 3.4.2 The general case: numerical results.

The nontrivial equilibrium points of the system (3.4) are given by the ninth-degree equation (3.9). The coefficients (3.10) depend on the parameters  $g_i, c_{ij}$   $i, j = 1, 2$ , that is, four parameters. The mathematical solution is not possible for biological interpretation. We can obtain relevant information by applying various theorems (Cardano, Descartes, Sturm, Budan-Fourier), but the results do not show generalized biological interpretations.

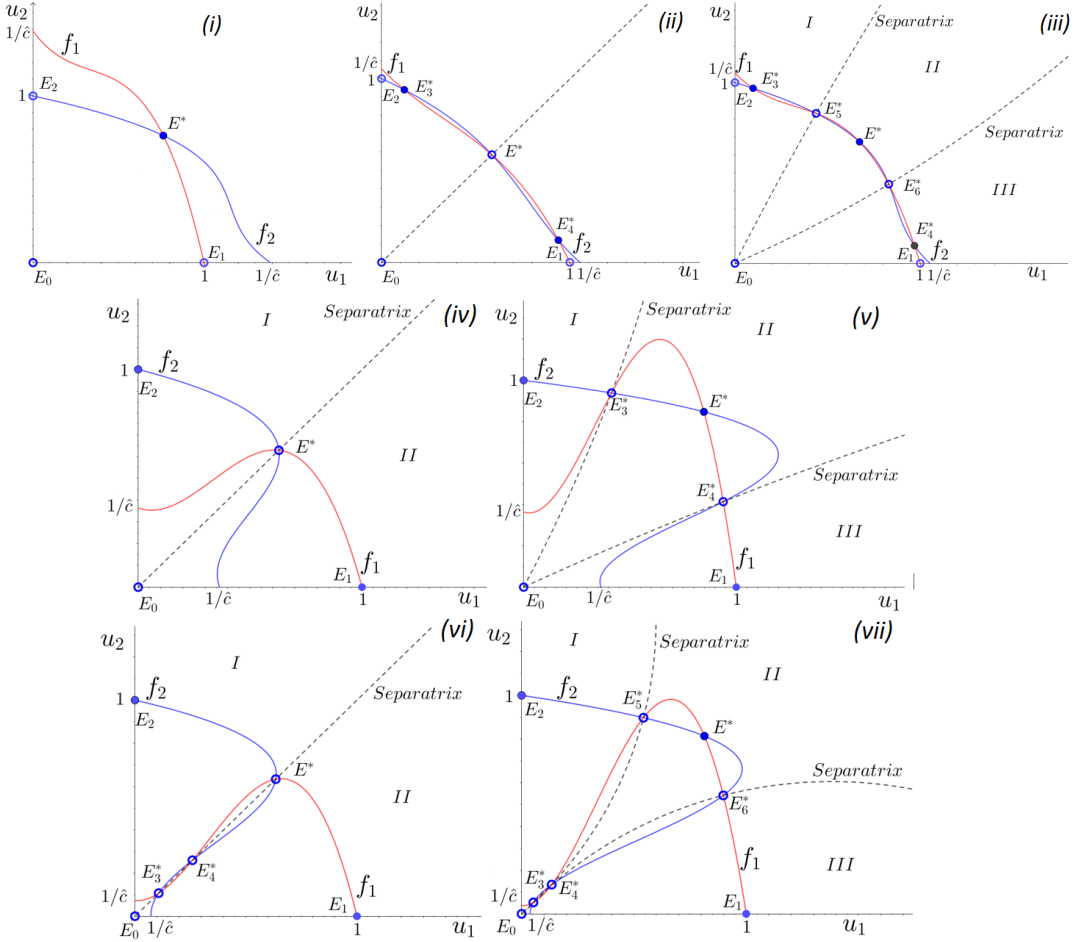
According to this, we perform a numerical analysis using an algorithm written the MATLAB software. Form the results found in the section 3.4.1 we decided to plot diagram that display, for fixed values  $g_i, i = 1, 2$ , the number of equilibrium points and its stability for  $c_{12}, c_{ij}$  ranging in given interval, as in figure 3.6.

As there are no analytical results for de complete model different from those already obtained at the beginning of section 3, we left the results of the numerical experiments to the discussion and conclusions section 5.

## 3.5 Discussion and conclusions.

In this chapter we summarize from a biological points of view the results obtained in the manuscript. We first interpret biologically the effect of considering group defense through the nullclines of system (3.4). Then, we focus on the case of one species displaying group defense. Next, we analyze the full model under symmetric competition conditions and the net effect on the full model.

### 3. Interference competition on group defense with Holling type IV competitive response



**Figure 3.3:** Possible phase portrait of sistem (3.4) under the symmetry conditions  $g_1 = g_2 \equiv g$  and  $c_{12} = c_{21} \equiv \hat{c}$ . Note that panels (iv) and (vi), and (v) and (vii) display the same biological outcome but the amount of unstable equilibrium points make each pair of them to be mathematically different.

In summary, we have found that group defense strategies improve the chances of coexistence, mainly by lowering the inter-species competition effect. This mechanism can be added to cooperation-competition effects [94] and accounting for interfering time [20] as mechanisms enhancing coexistence. We have also found a threshold value that makes emerge the effect of group defense. Finally, among the new scenarios found in the context of species coexistence, few of them are suitable to describe empirical observations of two species that can coexist in two different regimes (i.e., by-stable with two positive asymptotically stable equilibrium points) [36].

We have understood that in such competition where species interfere directly by obtaining food, survival or settling in a portion of habitat, the competition time can be carried out by an individual of a species or individuals group. firstly, We have found that the model proposed by

[20] is a particular case of the model derived herein when the consume interaction time among competitors is individual, ie, ( $ab = 0 \text{ due } T_{int} = 0$ ) and as a consequence, the classical model too when the interactions do not consume time, that is, ( $a_i = 0, \text{ due } T_{int} = 0$ ). Secondly, the new model presents a novel multi-stability scenarios.

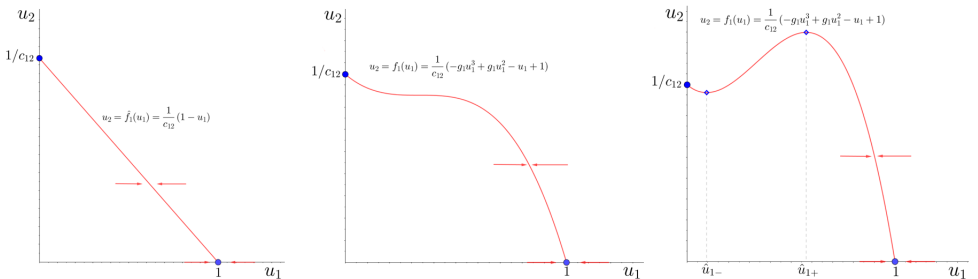
### 3.5.1 Interpreting nullclines.

Whether competing species manage to coexist or not depends on the balance between intra and inter species competition [72], [94]. We first analyze how group defense impacts on this balance though the nullclines of the model.

Let us recall that the bounded region defined by the axes and nullcline (lets say) of species 1 defines the values of the population size of species 2 that allow species 1 to keep growing. In the classical model ( $g_1 = 0$ ) these nullclines are straight lines with negative slope, meaning that the larger is the number of individuals of species species 1 is, the less tolerant (in order to keep growing) is to species 2, as shown in the left panel of figure 3.4.

However, as  $g_1$  becomes positive the nullcline is not a straight line anymore (center and right panels of figure 3.4). The effect is that the region of (both) species population sizes that allow species 1 to keep growing becomes larger (compared to the case  $g_1 = 0$ ). The “flat” region in the center panel of figure 3.4 can be understood as follows: the net effect of being more individuals is beneficial to species 1 since it reduces the effect of species 2 without increasing (significantly) the intra-species competition. This feature fails to be true before and after the flat region. At low densities there are too few individuals to face species 2 and intra species pressure ca be felt. After the flat region (and given that  $c \in (0, 3)$  is moderate) group defense does not since there are too few or too much individuals (not enough individuals to face species 2) and after balance intra species competition. Finally, for large enough values of  $c > 3$  group defense works much better, meaning that this cooperative behavior reduces intra species competition as well as reduces inter species competition, at least for  $u_1 \in (\hat{u}_{1-}, \hat{u}_{1+})$  (see the right panel of figure 3.4).

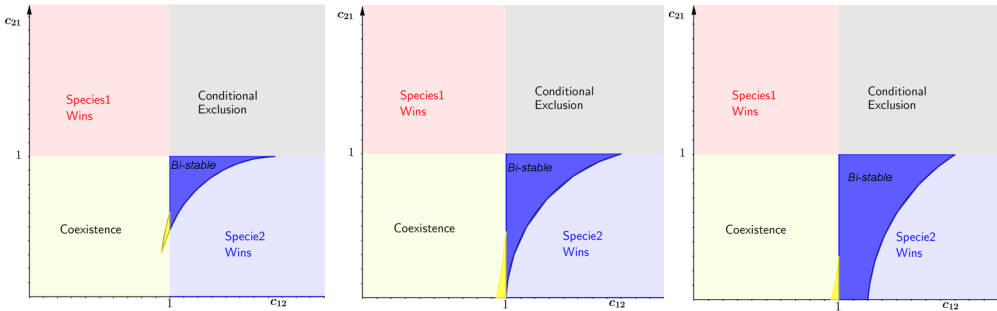
In a previous work [20] we observed that nullclines change from the classical ones (left panel, figure 3.4) to others more favorable, similar to that in the central panel of figure 3.4. However, such a consideration was not enough to revert the decreasing trend of nullclines as it happens in the case of group defense.



**Figure 3.4:** The nullcline  $u' = 0$  of system (3.4) for increasing values of  $g_1$ . Left,  $g_1 = 0$  (i.e., the classical Lotka-Volterra model(4.1)), center,  $g_1 = 0 \in (0, 3)$  and right,  $g_1 > 3$ .

3.5.2 Competitive Response on Group Defense in just one species

Assuming that species 1, under the competition mechanism  $0 < c_{ij} < 1, i \neq j = 1, 2$  corresponds to unconditional coexistence according to the model by Holling type II interference [20] and the classical model by interference. If  $g_{1-}^* < g_1 < g_{1+}^*$  corresponds to an unconditional coexistence where there are two non-trivial equilibrium points asymptotically stable, as established by Theorem (3.6). In other words, as species 1 has the ability to reduce a moderate competitive strength of species 2, there will be a dynamic scenario of unconditional coexistence figure(3.1-(i')). But, with group defense factor  $g_1 < g_{1-}^*$  and  $g_1 > g_{1+}^*$ , corresponds to the unconditional coexistence of the classic model figure ((4.6)-down panel) and in the phase portraits figure(3.1-(i)), where there is a non-trivial equilibrium asymptotically stable. we mean, that depending on the group defense factor  $g_i$  the group of individuals of species  $i$  can coexist versus the specie  $j$  regardless of the initial number of individuals of the group of species 1. Now, Assuming that species 1 with competitive strength  $0 < c_{21} < 1, c_{12} > 1, i = j = 1, 2$ . If  $g_{1-}^* < g_1$  corresponds to a conditional coexistence, This features takes the form of bi-stable conditional coexistence in favor of the group of individuals of species 1. That is, species will coexist if the initial number of group individuals of species 1 is large enough while, otherwise, species 1 will go extinct (see the dark blue region in figure 3.5). The larger is  $g_1$ , the ability of the group of individuals of species 1 of avoid species 2 competitive strength due to priority effects, the larger is the range of parameters values that enable bi-stable conditional coexistence in favor of species 1, as displayed in figure 3.5.



**Figure 3.5:** Competition outcomes of system (3.5) as function of competitive strengths  $c_{12}, c_{21}$  for increasing values of  $g_1$  (from left to right). The color is de same as in classical model figure 4.6 except the dark blue and yellow regions that represents bi-stable conditional coexistence and unconditional coexistence with two global attractor in the positive cone. The above shape is based on numerical calculations with the code source available in [19] and has been edited to improve it. Parameter values are  $c_{12} > 0, c_{21} < 3$  and  $g_1 = 1.95, 2.45, 9$ .

3.5.3 Competitive Response on Group Defense on both species.

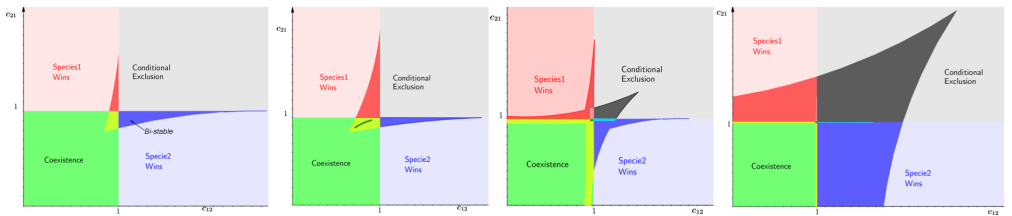
We turn our attention to the model with Holling type IV competitive response on group defense on both species. both in the previous case and the following show stable alternative states in which the spaces coexist unconditionally by the group defense mechanism. This is presented by Gundeson in [36], where alternative stable states have been described for a diverse variety of terrestrial and near terrestrial ecosystems, where periodic changes from one state to another are mediated by changes in slow processes that suddenly trigger a process fast (response or



escape from a state). such is the case of the Sea otters, sea urchin, find kelp forests [30]. In our framework it can be described as follows. We have first analyzed a particular case symmetric competition scenarios. In symmetric competition (Let recall that  $g_1 = g_2 = c$ ,  $c_{12} = c_{21} = \hat{c}$ ), we have found that the ability the group defense factor benefits coexistence and it help news dynamical scenarios. First, if the competitive strengths are less than 1, then there exists  $k = 1, 2$  or 3 attractors in the positive cone depending on the value of parameter  $c$  allowing unconditional global coexistence. If  $\hat{c} \in (0, \frac{8}{9})$  there exist a global positive attractor and unconditional global coexistence remains for all values of  $c > 0$ . But, if the competitive strength  $\hat{c} \in (\frac{8}{9}, 1)$  there exist  $k = 1, 2$  or 3 attractors as illustrate in the figure (see top figure (3.3)). If  $\hat{c} \in (1, \infty)$  theorem (3.8 and 3.10) tell us that both species can coexist and the tri-stable conditional coexistence if  $c \in (c_-^{**}, \infty)$ . In words, Species will coexist if the initial number of group of individuals of species 1 is large enough, otherwise, any of them goes extinct. On the other hand, the defense group factor  $c$  allow that the a group of individuals of one of the species compete in such a way as to limit the competitor's fighting effect to coexist in different state.

Figure 3.2 allows us the states of stability under symmetric competition for different values of the competitive strength  $\hat{c}$  and the factor  $c$ . For moderate values of inter-specific competitive ( $\frac{8}{9}, 1$ ) we can be in different states unconditionally stable as  $c$  grows, i.e., for values of  $c$  below the curve  $c_-^{**}(\hat{c})$  has a global stability, but for  $c$  values between the curves  $\hat{c}_-^{**}(\hat{c})$  and  $c_+^{**}(\hat{c})$  has an unconditional bi-stability (yellow). when it values is above  $\hat{c}_+^{**}(\hat{c})$  it can result in unconditional tri-stability (dark green) or again global stability. When the inter-specific competitive  $\hat{c}$  is greater than 1, the competition can be conditional coexistence or conditional exclusion. For values of  $\hat{c} \in (1, \infty)$  and  $c$  below the curve  $c_+^{**}(\hat{c})$  both species are in conditional exclusion region, but when  $c > c_+^{**}(\hat{c})$  is in conditional coexistence region. In words, as both groups of individuals of species grow, the ability to limit competitive strength becomes greater, where the exclusion condition changes to conditional coexistence, i.e., that either species coexistence or any of them go extinct.

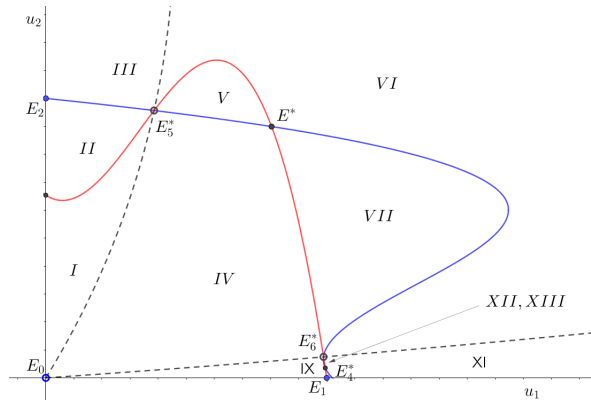
**Numerical results.** Considering particular conditions by restricting the parameters helps to obtain analytical interpretation biologic. it is evident that these particular results or cases do not differ qualitatively the generality of the model (3.4). We completed the analysis via numerical simulations (the source code can be found in [19]).



**Figure 3.6:** Competition outcomes of system (3.4) as function of competitive strengths  $c_{12}, c_{21}$  for increasing values of  $g_1$  and  $g_2$  (from left to right). The color is de same as figure 3.5 except the dark blue, pink and cian color's regions that represents 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 (being two of them asymptotically stable). the above shape is based on numerical calculations with the code source available in [19] and has been edited to improve it. Parameter values are  $c_{12} > 0$   $c_{21} < 4$  and  $g_1 = 1.9, 3.8, 5.8, 15$ ;  $g_2 = 1.5, 4.4, 6.4, 10$ .

We have found that when both species have the ability to reduce competitive pressure in groups, new zone of unconditional coexistence and bi-stable conditional coexistence appear

### 3. Interference competition on group defense with Holling type IV competitive response



**Figure 3.7:** Phase portrait in the numerical simulation scenario that display a new tri-satbility conditional coexistence outcome. The trapping regions II, V, VII, XII, and XIII can be analyzed as in section 3 and 4. It shows the steady state that describes tri-stable conditional coexistence.

(Figure 3.5: Yellow and dark blue regions). The zones are generated by the condition of the theorems 3.6 and 3.5. The Yellow region describes the condition where two steady states appear globally stable. Another region of coexistence appear (Dark black, Figure 3.6), where region is characterized by showing the tri-stable of conditional coexistence as can also be observed in [20]. The case of symmetric competition illustrates the above scenario shown in theorem 3.8 and 3.10 (see Figure 3.3). The Pink and Cain Regions show a case of tri-stable conditional coexistence. Figure 3.7 shows the phase portrait to the case cain color region in figure 3.6 that is a different case of the system (3.4) under symmetric competition. In words, as an individuals group of species 1 grows, but not enough to limit the interference competition, so the individuals' group of the species 2 wins. Then, both species can coexist depending on the range of parameter values and initial values.

# Modeling interference competition on sessile populations

In this work, we consider interference competition between two non-mobile living being populations (sessiles), in which individual species interaction dynamics take into account in this study, under feature that with occupying an area  $S$ , it follows that the species of the population  $i$  found in the periphery or neighborhood of their environment are proportional to the perimeter of the patch where the culture is located whose length depends on  $\sqrt{S}$ . Our main results show when a sessile population competes with a mobile population, all the competitive outcomes of the classical model are possible. Besides, conditional bi-stable coexistence in favor of the sessile population is possible, meaning that both a semi-trivial equilibrium and a coexistence equilibrium are (locally) asymptotically stable. Thus, whether the sessile population wins or both populations coexists depend on priority effects (the initial amount of individuals of each population). Besides, When both competing populations are sessile only species exclusion due to priority effects or conditional tri-stable coexistence is possible.

### 4.1 Introduction

A key factor when modeling community dynamics is that of how interactions take place. The vast majority of the research on community models, that follow in the wake of Lotka and Volterra [69], considers that individuals are well mixed and that any one of them can interact with all the rest. Interestingly, epidemic and eco-epidemic models do take into account such a major feature distinguishing the type of transmission [13, 59], that is closely related to the way individuals interact. Recently, [1, 6, 10, 46] addressed a series of community models that implement social structure which determines how populations interact with each other.

In this paper we consider interference competition between two non mobile living being populations, for which individual interaction dynamics is definitely different from mobile living beings [83]. Plants, of course, do belong to this category. Sessile species competition has been also reported in fungi [75], sponges [91], corals [14, 35, 41], giant clams, barnacles [23] or most of bivalves [84] are other examples, along with microorganism that grew up in colonies [57].

We thus consider two populations that homogeneously occupy two neighboring territories, but do not mix with each other, at least not significantly. Interactions among the two species' population can only occur through the common boundaries of the two cultures in consideration, that border each other (which may consist also of islands or other geometrical shapes).

Also, this consideration leads us to replace the classical 1-1 interactions among individuals of the same species with just those with the most immediate neighbors of a single individual. We thus prevent that one individual can compete with all other individuals in the population that are in far away locations.

The dynamics of interference competition is driven by the balance between intra and inter-species competition (when the model is written in terms of *explicit carrying capacities*) [83, 94] or competitive strengths (if the model is formulated with *emerging carrying capacities*) [16, 43, 76] that we prefer (see [45]). Anyway, the common interpretation of the early theory of competition [32, 56, 87] is that coexistence results when intra-species competition limits species' density more strongly than inter-species competition. In the present model competition is by far different than in the classical model, since 1-1 interactions are precluded. In particular, both intra and inter species competition are relaxed. Therefore, we expect competition outcomes to be different than in the classical model and recent extensions [20, 21]. Indeed, interactions seem to be milder in the model we present herein, so that we expect to find that species coexist more likely.

Our main results are the following. When a sessile population competes with a mobile population, all the competitive outcomes of the classical model are possible. Besides, conditional bi-stable coexistence in favor of the sessile population is possible, meaning that both a semi-trivial equilibrium and a coexistence equilibrium are (locally) asymptotically stable. Thus, whether the sessile population wins or both populations coexist depend on priority effects (the initial amount of individuals of each population).

When both competing populations are sessile only species exclusion due to priority effects or conditional tri-stable coexistence (coexistence or one species exclusion due to priority effects) are possible.

The manuscript is organized as follows: in next section 4.2 we transcribe to equations those peculiarities derived from the fact that individuals do not move and populations interact at the

boundary of its respective domains. Subsequently, we analyze the competition in section 4.3. Finally, we discuss the results achieved in section 4.4.

## 4.2 The competing sessile populations model

The departure model is the classical Lotka-Volterra competition model with *emergent carrying capacities* [16, 43, 76] rather than explicit carrying capacities [69, 94]:

$$\begin{cases} x_1' = r_1 x_1 - a_{11} x_1^2 - a_{12} x_1 x_2 \\ x_2' = r_2 x_2 - a_{22} x_2^2 - a_{21} x_1 x_2 \end{cases} \quad (4.1)$$

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 modeling of sessile populations is thus rather different from the classical interacting populations made of (mobile) animals. As assumed in other investigations concerning herds of herbivores and their predators, [1, 6] or interference competition [64], we assume here that interactions among different species, uniformly located in specific territories, occur through their common boundaries, as stated above. This territory can be assumed either circular or squared.

Thus, we consider both  $x_1$  and  $x_2$  to represent the density of the populations, that is, the number of individuals per surface unit, with occupying an area  $S$ , it follows that the species of the population  $i$  found in the periphery or neighborhood of their environment are proportional to the perimeter of the patch where the culture is located whose length depends on  $\sqrt{S}$ . They are therefore in number proportional to the square root of the density, i.e. to  $\sqrt{x_i}$ ,  $i = 1, 2$ . In fact, different shapes could be accommodated by taking a different exponent, other than one half, in the model formulation, but in part based also on the results of [18] for which no fundamentally different results arise, and for simplicity sake, we confine ourselves to the circular assumption. This, as mentioned, entails the use of the exponent one half in the model formulation. We next detail intra and inter species interaction terms:

- Inter-species interactions take place on the boundary of each species domain. In view of the previous discussion, as individuals are assumed to be homogeneously distributed, the interaction between species  $x_i$  and  $x_j$  takes the following form:

$$- d a_{ij} \sqrt{x_i} \sqrt{x_j}, \quad (4.2)$$

where the sign  $-$  denoting for interactions that damage the population under consideration,  $a_{ij}$  stands for species competition coefficient and  $d$  is a constant that scales competition to the fraction of the common perimeter. If  $d = 0$  then species does not interact (no common boundary) although the meaning of other values depends on the geometry of cultures. Therefore,  $d_i a_{ij}$ ,  $i \neq j$  stands for inter-species competition and includes information the fraction of the boundary where competition takes place, so that its interpretation is slightly different from the interaction coefficients of the classic model. In general  $d_i \neq d_j$ .

- For intra species dynamics, we must include the growth rate and possibly intra species competition:

$$x_i' = \hat{r}_i x_i - b_i a_{ii} x_i \sqrt{x_i} \quad (4.3)$$

## 4. Modeling interference competition on sessile populations

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where  $\hat{r}_i$  stands for the net intrinsic growth rate,  $a_{ii}$  is the intra-species competition rate, and  $b$  will be described below. Equation (4.3) is a modification of the well known logistic growth that takes into account that sessile living being stand still and interact only with their most immediate neighbors, as discussed above. Thus, a given individual competes with the nearby ones, that we assume are located at the boundary layer of its “vital space”, that is, a circle area around the individual. Assuming that individuals are homogeneously distributed, the boundary of each individual’s *vital space* is proportional to the boundary of the territory occupied by this species, i.e., proportional to  $\sqrt{x}$ . In this context,  $b_i$  in (4.3) stands for that proportion between the local boundary and the perimeter occupied by the entire population, so that  $b_i > 0$ . It is assumed to be the same for all individuals of the same species.

Merging (4.3) and (4.2) yields the competing sessile populations model

$$\begin{cases} x'_1 = \hat{r}_1 x_1 - b_1 a_{11} x_1 \sqrt{x_1} - d_1 a_{12} \sqrt{x_1} \sqrt{x_2}, \\ x'_2 = \hat{r}_2 x_2 - b_2 a_{22} x_2 \sqrt{x_2} - d_2 a_{21} \sqrt{x_1} \sqrt{x_2}, \end{cases} \quad (4.4)$$

that is the model we are going to analyze next.

### 4.2.1 The single population case.

The single population case has been briefly examined also in [46], as a motivation for further changes in the formulation of herd behavior models. Here we focus on a population that does not move. For one single plant living in a plantation, therefore surrounded just by other plants of the same species, the model becomes simply:

$$x' = \hat{r}x - bax\sqrt{x}. \quad (4.5)$$

Clearly, of the two possible equilibria, the origin is unstable while the population thrives at level

$$x^* = \frac{r^2}{b^2 a^2}. \quad (4.6)$$

In the same conditions, the classical logistic equation instead would state that the population settles at

$$x^c = \frac{r}{a}. \quad (4.7)$$

So, qualitatively the two models behave in the same way. However, whether a single plant living in a wood or plantation is better off than a corresponding animal individual living amidst his own consimilars, depends on the ratio between its net reproduction rate and the intraspecific competition rate. If the former exceeds the latter, the level at which the vegetable species settles is certainly higher than the corresponding animal population.

## 4.3 Analysis of the model

Whenever we consider a single population, system (4.4) reduces to a logistic like model, that is well behaved. Therefore, the axes are forward invariant to system (4.4). Indeed

**Theorem 4.1.** *The positive solutions of system (4.4) are also forward bounded.*

**Proof:** Note that

$$x'_i = \hat{r}_i x_i - b_i a_{ii} x_i \sqrt{x_i} - d_i a_{ij} \sqrt{x_j} \sqrt{x_i} < (\hat{r}_i x_i - a_{ii} x_i \sqrt{x_i}) < 0$$

for  $x_i > (r/a_{ij})^2$ . In particular, it corresponds to having on the positive cone the flow entering a suitable box  $B$  with one corner located at the origin and the opposite one at the point  $V = \left( (r_1/d_1 a_{12})^2, (r_2/d_2 a_{21})^2 \right)$ . ■

**Remark:** we need special care in treating vanishing populations when we change the variables and dimensionalized parameters on the system (4.4) to obtain the auxiliary system more latter, because we eliminate the singularity. Therefore, we have to turn to the original formulations (4.4) to study for trivial and semi-trivial equilibrium points, this reasoned as in [10]. In this sense, we will study the trivial and semi-trivial equilibria with model (4.4). The trivial and semi-trivial equilibrium are the following:

$$E_0 = (0, 0), \quad E_1 = \left( \left( \frac{r_1}{b_1 a_{11}} \right)^2, 0 \right), \quad E_2 = \left( 0, \left( \frac{r_2}{b_2 a_{22}} \right)^2 \right) \quad (4.8)$$

Note also that there are squared root terms in system (4.4), so that the stability of the trivial and semi-trivial equilibrium points (4.8) can not be assessed using the Jacobian matrix which, in turn, works when dealing with coexistence equilibria. However, square roots make the Jacobian matrix to be involved; we next introduce an equivalent equations system to overcome such a problem.

### 4.3.1 Mobile and non-mobile population model.

Before analyzing the general system model (4.4), we focus that we called a special system in which a population mobile individuals species and sessile individuals species are analyzed. Thus, system (4.4) reads as

$$\begin{cases} x'_1 = r_1 x_1 - a_{11} x_1^2 - a_{12} x_1 x_2, \\ x'_2 = r_2 x_2 - a_{22} b_2 x_2 \sqrt{x_2} - a_{21} x_1 x_2. \end{cases} \quad (4.9)$$

Reasoning as for system (4.4), it is easy to realize that (4.9) is well behaved. We next analyze the existence of equilibrium points and the long term behavior of the solutions of system (4.9). We first re-write system in a more convenient (4.9). Indeed, system (4.9) is equivalent to

$$\begin{cases} x'_1 = r_1 x_1 \left( 1 - \frac{a_{11}}{r_1} x_1 - \frac{a_{12}}{r_1} x_2 \right), \\ x'_2 = r_2 x_2 \left( 1 - \frac{a_{22}}{r_2} b_2 \sqrt{x_2} - \frac{a_{21}}{r_2} x_1 \right). \end{cases} \quad (4.10)$$

We re-scale the above system with special change variable and parameters, namely  $w_i = \frac{a_{ii}}{r_i} x_i$ ,  $c_{ij} = \frac{a_{ij} r_j}{a_{jj} r_i}$ , to obtain

$$\begin{cases} w'_1 = r_1 w_1 (1 - w_1 - c_{12} w_2), \\ w'_2 = r_2 w_2 \left( 1 - b_2 \sqrt{\frac{a_{22}}{r_2}} \sqrt{w_2} - c_{21} w_1 \right) \end{cases} \quad (4.11)$$

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A further re-scaling in system (4.11) given by  $\hat{w}_2 = \frac{a_{22}}{r_2} w_2$ ,  $\hat{c}_{12} = \frac{r_2}{a_{22}} c_{12}$ , that yields the so-called special auxiliary system:

$$\begin{cases} w_1' = r_1 w_1 (1 - w_1 - \hat{c}_{12} \hat{w}_2), \\ w_2' = r_2 \hat{w}_2 (1 - b_2 \sqrt{\hat{w}_2} - c_{21} w_1) \end{cases} \quad (4.12)$$

#### Equilibria

The trivial and semi-trivial equilibrium of system (4.12) are:

$$E_0 = (0, 0) \quad E_1 = (1, 0) \quad \text{and} \quad E_2 = \left(0, \frac{1}{b_2^2}\right) \quad (4.13)$$

We consider the nullclines of system (4.12), that are given by

$$\hat{w}_2 = f_1(w_1) = \frac{1 - w_1}{\hat{c}_{12}}, \quad \hat{w}_2 = f_2(w_1) = \frac{(c_{21} w_1 - 1)^2}{b_2^2}.$$

The coexistence equilibria are denoted by  $E_3^\pm = (w_1^\pm, f_1(w_1^\pm))$ , and they are the intersection of the nullclines, in this case a curve and a straight line. These solutions can be obtained as the roots of the following equation:

$$P_{sc}(w) = \frac{1}{\hat{c}_{12} b_2^2} [-\hat{c}_{12} c_{21}^2 w_1^2 + (2\hat{c}_{12} c_{21} - b_2^2)w + (\hat{c}_{12} - b_2^2)],$$

where,

$$w_1 = \frac{2\hat{c}_{12} c_{21} - b_2^2 \pm b_2 \sqrt{4\hat{c}_{12} c_{21} (c_{21} - 1) + b_2^2}}{2\hat{c}_{12} c_{21}^2} \quad (4.14)$$

Analyzing the discriminant of expression (4.14), we can find the real roots in the positive cone. The following Lemma 4.1 and Theorem 4.2 summarize these conditions.

**Lemma 4.1.** *Consider the function*

$$c_{21} = \psi_{b_2}(\hat{c}_{12}) := \frac{\hat{c}_{12} + \sqrt{\hat{c}_{12}(\hat{c}_{12} - b_2^2)}}{2\hat{c}_{12}}, \quad (4.15)$$

then,  $\psi_{b_2}$  is an unimodal function such that:

$$1. \quad c_{21}^* = \psi_{b_2}(1) = \frac{1 + \sqrt{1 - b_2^2}}{2} \quad \text{and} \quad \lim_{\hat{c}_{12} \rightarrow +\infty} \psi_{b_2}(\hat{c}_{12}) = 1$$

$$2. \quad \text{The Domain } \psi_{b_2} := \{x \in \mathbb{R}^+ \mid 1 \leq x < \infty\}$$

**Proof:** It follows from direct calculations. ■

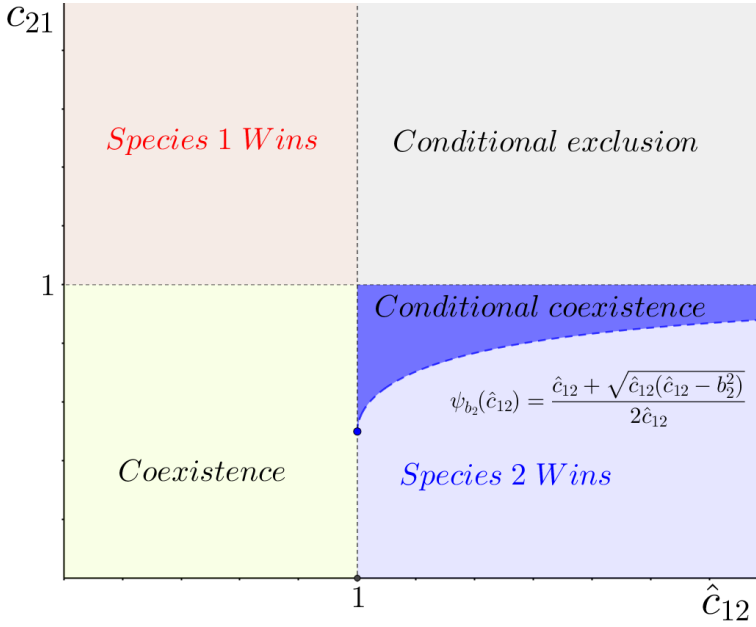
Whether there is none, one or two equilibrium points can be derived in terms of the discriminant of (4.14) and the quantities defined in the previous Lemma 4.1.

**Theorem 4.2.** *Consider system (4.12) and function (4.15). Also, we denote the discriminant of equation (4.14) as*

$$D := 4\hat{c}_{12} c_{21} (c_{21} - 1) + b_2^2 \quad (4.16)$$

Then,





**Figure 4.1:** Competition outcomes special competition model as function inter-species interaction taking into account intra-species interaction of system(4.9).

1. System (4.12) has no equilibrium points in the positive cone if either
  - (a)  $D < 0$ , see see middle right panel in figure 4.2.
  - (b) Both  $1/c_{21} < 1$  and  $1/\hat{c}_{12} > 1/b_2^2$  hold, see top left panel in figure 4.2. An alternative formulation of the above inequalities is  $\hat{c}_{12} < 1$  and  $c_{21} > 1$ .
2. System (4.12) possesses a single equilibrium point in the positive cone (we do not consider the degenerated case  $D = 0$ ) if either
  - (a) Both  $1/\hat{c}_{12} < 1 < b_2^2$  and  $1/c_{21} < 1$  hold, see top right panel in figure 4.2. An alternative formulation of the above inequalities is  $\hat{c}_{12} > 1$  and  $c_{21} > 1$ .
  - (b) Both  $1/\hat{c}_{12} > 1/b_2^2$  and  $1/c_{21} > 1$ . An alternative formulation of the above inequalities is  $\hat{c}_{12} < 1$  and  $c_{21} < 1$ .
3. System (4.12) has two equilibrium points in the positive cone if  $\hat{c}_{12} > 1$  and  $\psi_{b_2}(\hat{c}_{12}) < c_{21} < 1$  hold.

**Proof:** It follows from direct calculations on (4.14) and (4.16) and geometrical considerations on the intersection of  $f_1$  and  $f_2$  with the axes. ■

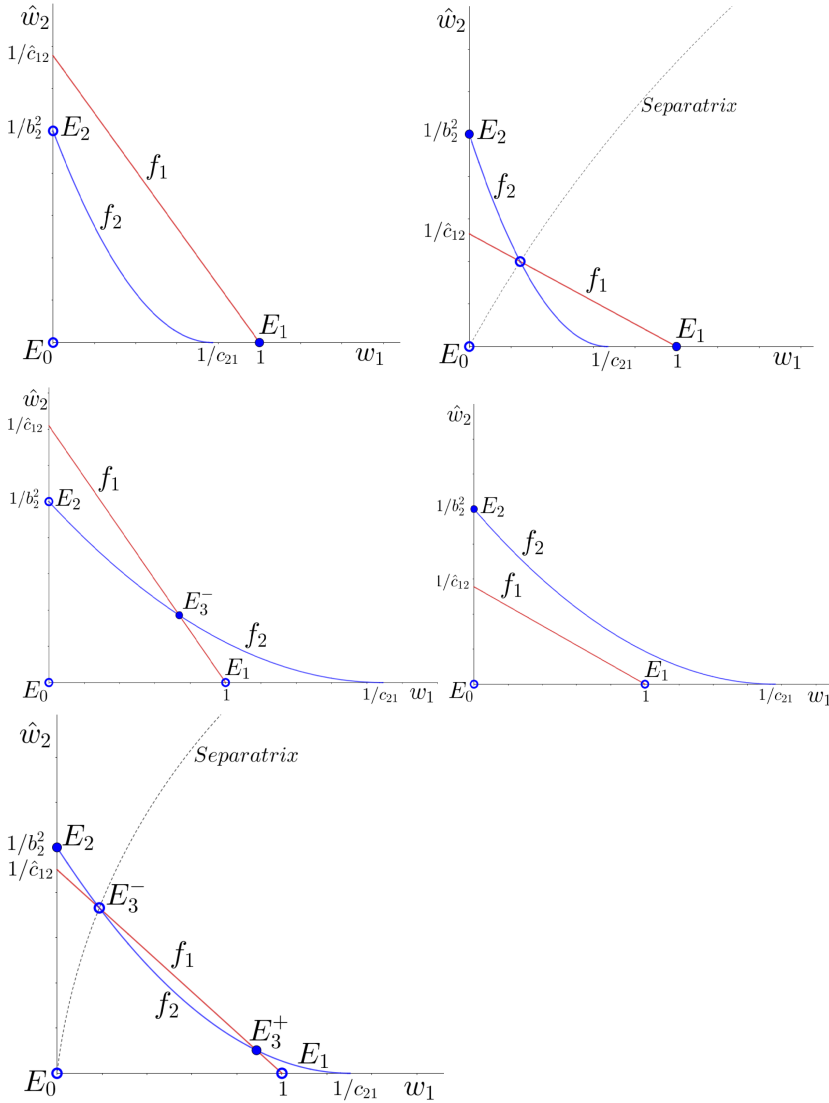
### Stability

We focus now on the stability of the existing equilibrium points.

**Theorem 4.3.** Consider system (4.12), assuming that  $r_1 > 0$  and  $r_2 > 0$ . Then,

1. The origin is always unstable.

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**Figure 4.2:** Possible phases portrait special competition model (4.9).

2. Assume now  $\hat{c}_{12} > 1$  and  $c_{21} > 1$ . Then there exists a single coexistence equilibrium point  $E_3^+$ , that is unstable. There exists a separatrix line passing through  $E_3^+$  and the origin that defines the basins of attraction of  $E_1$  and  $E_2$ .
3.  $E_1$  is globally asymptotically stable if, and only if,  $0 < \hat{c}_{12} < 1$  and  $c_{21} > 1$ .
4.  $E_3^-$  is globally asymptotically stable if, and only if,  $0 < \hat{c}_{12} < 1$  and  $0 < c_{21} < 1$ .
5. Finally, assume now  $0 < c_{21} < 1$  and  $\hat{c}_{12} > 1$ . Then,

- (a)  $E_3^+$  and  $E_2$  are locally asymptotically stable while  $E_-^c$  are unstable. There exist separatrix passing through the origin and  $E_-^c$  and define the basis of attraction of  $E_2$ , and  $E_3^+$ , if and only if,  $\hat{c}_{12} > 1$  and  $\psi_{b_2}(\hat{c}_{12}) < c_{21} < 1$ .
- (b)  $E_2$  is globally asymptotically stable if, and only if,  $0 < c_{21} < \psi_{b_2}(\hat{c}_{12})$  and  $\hat{c}_{12} > 1$ .

**Proof:** Let us consider the Jacobian matrix of (4.9)

$$JF(w_1, \hat{w}_2) := \begin{pmatrix} r_1(1 - w_2 - \hat{c}_{12}w_2) & -r_1\hat{c}_{12}w_1 \\ -r_1c_{21}\hat{w}_2 & r_2(1 - b_2\sqrt{\hat{w}_2} - c_{21}w_1) - \frac{1}{2}r_2b_2\sqrt{\hat{w}_2} \end{pmatrix}$$

Thereby, we analyzing the characteristic equation and applying the Routh-Hurwitz criterion to the equilibrium points:

1. At the origin  $E_0$ , we find that the eigenvalues of  $JF(E_0)$  are  $\lambda_1 = r_1$ ,  $\lambda_2 = r_2$  so that  $E_0$  is unstable provided that  $r_i > 0$ , for  $i = 1, 2$ .
2. It holds because the eigenvalues of  $JF(E_1)$  are  $\lambda_1 = -r_1$ ,  $\lambda_2 = r_2(1 - c_{21})$ . Therefore,  $E_3^-$  is unstable and  $E_2$  and  $E_1$  are locally asymptotically stable; in such case, exist a separatrix line passing through  $E_3^-$  and the origin that defines the basins of attraction of  $E_1$  and  $E_2$ .
3. Direct calculations yield the eigenvalues of  $JF(E_2)$ ,  $\lambda_1 = -r_2(1 - \frac{3}{2}b_2)$ ,  $\lambda_2 = r_1(1 - \hat{c}_{12})$ . The statement implies that  $E_2$  is stable while  $E_1$  is unstable. Also theorem 4.2 show that no equilibrium points exist in the positive cone, and the flow of the system makes  $E_2$  globally asymptotically stable.
4. This statement follows by an standard analysis of the flow of the system.
5. We focus first in assessing the stability in case of having two coexistence equilibrium points. This dynamical scenario may arise, when coefficients vary, essentially in two different ways. On the one hand, when  $D$  changes from being negative to positive. On the other hand, already there exists a single coexistence equilibrium point and the  $x_2$ -nullcline  $f_2$  crosses one of the semi-trivial equilibrium points in such a way that a second one appears. The dynamical scenario in the same, no matter how we get to.

Let us rewrite the Jacobian matrix in a more convenient form. System (4.12) is of the form  $w'_i = w_i f_i(w_i, w_j)$ , so that at any coexistence equilibrium point  $E = (E_1, E_2)$  it follows that  $f_1(E) = 0 = f_2(E)$ . This feature yields that

$$JF(E) := \begin{pmatrix} -r_1E_1 & -r_1\hat{c}_{12}E_1 \\ -r_2c_{21}E_2 & -\frac{1}{2}r_2b_2\sqrt{E_2} \end{pmatrix} \quad (4.17)$$

From expression (4.14) at  $D = 0$ , direct calculations yield that the characteristic polynomial of (4.17) at the equilibrium point that arises when  $f_1$  and  $f_2$  collide is

$$\lambda^2 + \left( \frac{b_2^2(c_{21}r_2 - 2r_1) + 4\hat{c}_{12}c_{21}r_1}{4\hat{c}_{12}c_{21}^2} \right) \lambda. \quad (4.18)$$

Thus, one eigenvalue is  $\lambda_1 = 0$  and the other one,  $\lambda_2$ , is negative (because of the hypotheses of this statement); in particular, both eigenvalues are simple. Thus, the eigenvalues are continuous under small perturbations of the parameters involved in expression (4.17). As  $E_3^-$  and  $E_3^+$  appear  $\lambda_2$  keeps being negative in the corresponding Jacobian matrices

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while  $\lambda_1$  becomes negative for  $JF(E_3^-)$  and positive for  $JF(E_3^+)$ , what follows from an standard analysis of the flow of the system after the bifurcation takes place.

The second statement of 5. can be proved as 4.

■

### 4.3.2 Sessile general model

System (4.4) can be rewritten in a more convenient form introducing new variables and re-scaling coefficients by setting

$$x_i = z_i^2, \quad r_i = \frac{\hat{r}_i}{2}, \quad c_{ii} = b_i a_{ii}, \quad c_{ij} = \frac{d_i a_{ij}}{2}, \quad i, j = 1, 2. \quad (4.19)$$

that yield the so-called *auxiliary system*:

$$\begin{cases} z_1' = r_1 z_1 - c_{11} z_1^2 - c_{12} z_2 \\ z_2' = r_2 z_2 - c_{22} z_2^2 - c_{21} z_1 \end{cases} \quad (4.20)$$

It is apparent that the no-negative semi-axes are not invariant for the flow of system (4.20), so that this system does not help in assessing the stability of the trivial and semi-trivial equilibrium points.

As before we address first the existence of equilibrium points and then analyze its stability,

#### Equilibria.

As we mentioned earlier the trivial and semi-trivial equilibria of system (4.4) are given by (4.8). As for the coexistence equilibria, we consider the nullclines of the auxiliary system (4.20) corresponding to system (4.4), that are given by

$$z_2 = f_1(z_1) = z_1 \frac{r_1 - c_{11} z_1}{c_{12}}, \quad z_1 = f_2(z_2) = z_2 \frac{r_2 - c_{22} z_2}{c_{21}}.$$

The nullclines cross at the origin and its curvature and location imply that they meet up to three times or none on the positive cone, see figure 4.3, and the discussion below and section 4.4, discussion and conclusion.

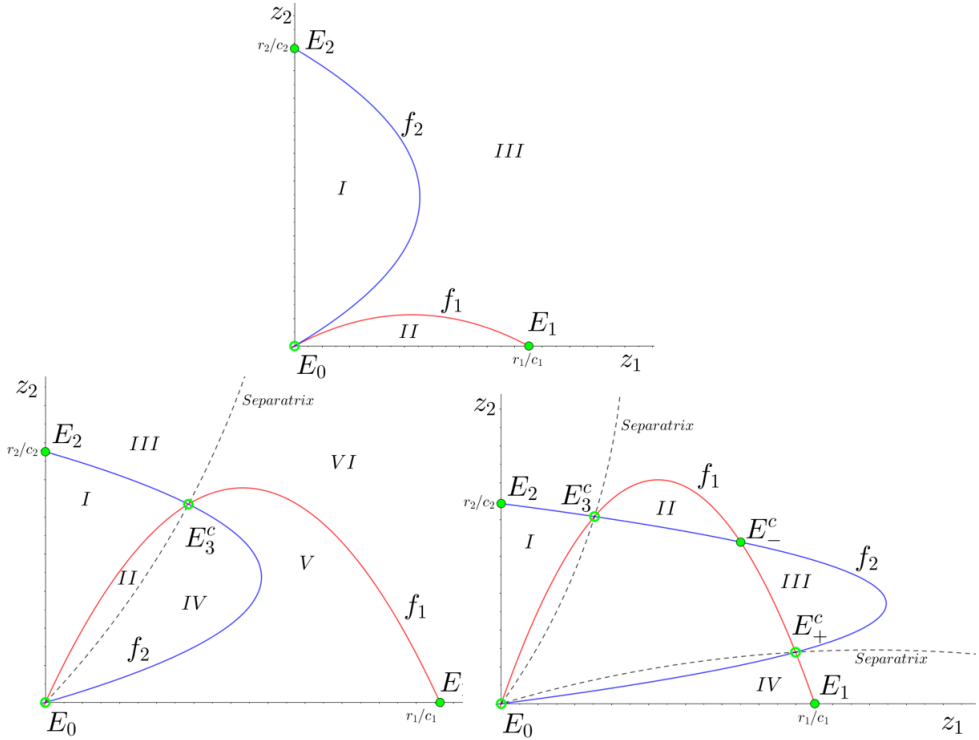
However, system (4.4) may exhibit two additional coexistence estates in the positive cone. Let us substitute the second equation on the first one we obtain a fourth-degree equation:

$$Q_c(z_1) = \frac{1}{c_{12}^2} z_1 P_c(z_1) = 0. \quad (4.21)$$

where  $Q_c(z_1) = f_2(f_1(z_1))$  and

$$P_c(z_1) = c_2 c_1^2 z_1^3 - 2c_2 c_1 r_1 z_1^2 + (c_1 c_{12} r_2 + c_2 r_1^2) z_1 + c_{12} (c_{12} c_{21} - r_1 r_2).$$

The geometry of the phase portrait implies that coexistence equilibrium lay on the box with the origin and  $(r_1/c_1, r_2/c_2)$  as opposite vertexes. Therefore, we use the Sturm's Theorem to



**Figure 4.3:** Possible phase portrait of the corresponding auxiliary competition model (4.20). Left panel: for the parameter values  $r_1 = 0.8$ ,  $r_2 = 0.6$ ,  $c_{12} = 1.2$ ,  $c_{21} = 0.95$ ,  $c_1 = 0.47$ ,  $c_2 = 0.74$  the one-population equilibria are shown and the condition (4.25) hold. Central panel: for the parameter values  $r_1 = 1$ ,  $r_2 = 1$ ,  $c_{12} = 1.51$ ,  $c_{21} = 0.52$ ,  $c_1 = 0.66$ ,  $c_2 = 1.24$ , the condition (4.26) and (4.27) holds. The system exhibits the competitive exclusion principle, exactly as it happens for the classical model competition model, [5]. Right panel: this scenario represents the tri-stable scenario. It is obtained for the parameter values  $r_1 = 1$ ,  $r_2 = 1$ ,  $c_{12} = 0.28$ ,  $c_{21} = 0.13$ ,  $c_1 = 0.47$ ,  $c_2 = 0.74$  In this case either one of the population could outcompete the other one, or both can coexist. The ultimate outcome of the system is determined just by the set in which the initial conditions lie.

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account for the number of positive roots of equation  $P_c(z_1) = 0$ . Let us recall that the Sturm's sequence of equation  $P_c(z_1) = 0$  is given by

$$Seq_c(z_1) = \{P_c(z_1), P'_c(z_1), R_1(z_1), R_2(z_1)\},$$

where the second term is its derivative of  $P_c(z_1)$ , and the remaining terms  $R_i(z_1)$ ,  $i = 1, 2$ , are the remainder of the euclidean divisions:

$$R_1(z_1) = -\text{rem}(P_c(z_1), P'_c(z_1)), \quad R_2(z_1) = -\text{rem}(P'_c(z_1), R_1(z_1))$$

Then, evaluating each term of the  $Seq_c$  at the ends of interval  $[0, r_1/c_1]$  we get the number of positive roots of  $P_c(z_1) = 0$  as the number of changes of sign in  $Seq_c(0)$  minus the number of change of signs in  $Seq_c(r_1/c_1)$ . So, the actual Sturm's sequence is calculated on  $P_c(z_1)$  instead of on  $Q_c(z_1)$ . Direct calculations lead to

$$P'_c(z_1) = 3c_1^2c_2z_1^2 - 4c_1c_2r_1z_1 + c_1c_{12}r_2 + c_2r_1^2 \quad (4.22)$$

$$R_1(z_1) := -\left(\frac{2r_2c_1c_{12}}{3} - \frac{2c_2r_1^2}{9}\right)z_1 - \frac{9c_1c_{12}^2c_{21} - 7c_1c_{12}r_1r_2 + 2c_2r_1^3}{9c_1} \quad (4.23)$$

$$R_2(z_1) := -\frac{9c_1c_{12}^2(4c_1^2c_{12}r_2^3 + 27c_1c_{12}^2c_2c_{21}^2 - 18c_1c_{12}c_2c_{21}r_1r_2 - c_1c_2r_1^2r_2^2 + 4c_2^2c_{21}r_1^3)}{4(3c_1c_{12}r_2 - c_2r_1^2)^2} \quad (4.24)$$

**Theorem 4.4.** *System (4.4) has no equilibrium points in the positive cone if*

$$c_{12}c_{21} - r_1r_2 > 0 \quad (4.25)$$

**Proof:** Consider the Sturm's sequences  $Seq(0)$

$$P_c(0) = c_{12}(c_{12}c_{21} - r_1r_2), \quad P'_c(0) = c_1c_{12}r_2 + c_2r_1^2,$$

$$R_1(0) = \frac{-1}{9} \left( \frac{9c_1c_{12}^2c_{21} - 7c_1c_{12}r_1r_2 + 2c_2r_1^3}{c_1} \right)$$

and  $R_2(0)$  is that given by (4.24). On the other hand,  $Seq(r_1/c_1)$  consists of

$$P_c\left(\frac{r_1}{c_1}\right) = c_{12}^2c_{21}, \quad P'_c\left(\frac{r_1}{c_1}\right) = r_2c_1c_{12}, \quad R_1\left(\frac{r_1}{c_1}\right) = \frac{-c_{12}(9c_{12}c_{21} - r_1r_2)}{9}$$

and  $R_2(r_1/c_1)$  is, again, that given by (4.24), since it does not depend on  $z_1$ . Rearranging terms

$$R_2(0) = \frac{-9c_1c_{12}^2 [4(c_1^2c_{12}r_2^3 + c_2^2c_{21}r_1^3) + c_1c_2(27c_{12}^2c_{21}^2 - 18c_{12}c_{21}r_1r_2 - r_1^2r_2^2)]}{4(3c_1c_{12}r_2 - c_2r_1^2)^2}.$$

Note that it does not matter the sign of  $R_2(0) = R_2(r_1/c_1)$  since it is the same at  $Seq(0)$  and  $Seq(r_1/c_1)$ . Therefore, gathering signs yield  $Seq(0) = \{+, +, -, \text{sign}(R_2(0))\}$  and  $Seq(r_1/c_1) = \{+, +, -, \text{sign}(R_2(0))\}$ , which concludes the proof. ■

We carry on assuming that condition (4.25) fails. Solving equation (4.21) under the assumption that  $c_{12}c_{21} - r_1r_2 = 0$  yields two complex roots along with  $z_1 = 0$  as unique real root with multiplicity 2. Let us recall the fact that there exists an equilibrium point in the third quadrant when (4.25) holds. This equilibrium colides with the origin at  $c_{12}c_{21} - r_1r_2 = 0$  and appear in the positive cone as  $c_{12}c_{21} - r_1r_2$  becomes negative. Besides, the analysis of the Sturm's sequence for  $c_{12}c_{21} - r_1r_2 < 0$  yields that there exist at least one, and up to three, positive coexistence equilibrium points. Criteria leading to each outcome can be stated finding conditions that control the change of sign of the terms of the Sturm's sequence.

Finding out general conditions is hard, since the terms of  $Seq(0)$  and  $Seq(r_1/c_1)$  depend on up to 6 parameters. In any case, we shall equate to zero each term no sign-defined of the Sturm's sequence and solve each expression on one parameter to get conditions on the sign of each term. Solving the equations on  $c_i$  (resp.  $c_{ij}$ ) yield conditions for exclusion or conditional tri-stability that depend on the so-called handling time (resp., on the competition strength) of each species.

**Theorem 4.5.** *Consider system (4.4) and assume that*

$$c_{12}c_{21} - r_1r_2 < 0 \quad (4.26)$$

Then,

1. Assume that

$$9 < \frac{r_1r_2}{c_{12}c_{21}} \quad (4.27)$$

and consider the straight lines

$$c_2^\pm(c_1) = \frac{-27c_{12}^2c_{21}^2 + 18c_{12}c_{21}r_1r_2 + r_1^2r_2^2 \pm \sqrt{(c_{12}c_{21} - r_1r_2)(9c_{12}c_{21} - r_1r_2)^3}}{8c_{21}r_1^3} c_1 \quad (4.28)$$

on the  $c_1c_2$  parameter space, that show up from equating to zero  $R_2(0)$ . There lines define a sector region in the positive cone, see Figure 4.4. Then,

- (a) The slope of  $c_2 = c_2^\pm(c_1)$  is positive.
- (b) If  $(c_1, c_2)$  lies in between  $c_2 = c_2^\pm(c_1)$  then there exist three non-trivial equilibrium points  $E_\pm^c, E_3$  in the positive cone. Ordered by its first component,  $E_-^c < E_3^c < E_+^c$ .
- (c) If  $(c_1, c_2)$  does not lie in between  $c_2 = c_2^\pm(c_1)$  then there exists a single non-trivial equilibrium point  $E_3$  in the positive cone.

2. Besides, if condition

$$9 > \frac{r_1r_2}{c_{12}c_{21}} \quad (4.29)$$

holds, then there exists a single non-trivial equilibrium point  $E_3$  in the positive cone. If condition (4.29) is an equality,  $c_2^\pm$  collide in a single straight line. The outcome is the same also a single positive coexistence equilibrium point.

**Proof:** The equation  $R_2(0) = 0$  in  $c_2$  is a second order equation of the form  $-a(a_2c_2^2 + a_1c_2 + a_0) = 0$ . Solving such an equation in  $c_2$  and arranging terms yields expression (4.28). Note that condition (4.27) (that, in particular, entail (4.26)) ensures that the straight lines (4.28) are well defined, in the sense that the slopes are real (and not complex) numbers.

Note that  $a_0$  and  $a_2$  are positive; therefore, we need

$$a_1 = 27c_{12}^2c_{21}^2 - 18c_{12}c_{21}r_1r_2 - c_{12}^2c_{21}^2$$

#### 4. Modeling interference competition on sessile populations

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to be negative in order to solving  $R_2(0) = 0$  in  $c_2$  yields a positive root (indeed, two positive roots). Rearranging terms,  $a_1$  is equivalent to

$$a_1 = -(27c_{12}c_{21}(c_{12}c_{21} - r_1r_2) + r_1r_2(9c_{12}c_{21} - r_1r_2))$$

therefore, conditions (4.26) and (4.27) imply that  $a_1 > 0$ , that proves 1(a).

Let us recall that conditions (4.26) and (4.27) imply that  $Seq(0) = \{-, +, -, ?\}$  and  $Seq(r_1/c_1) = \{+, +, ?, ?\}$ , so that the only way of having three equilibrium points is that  $R_2(0) > 0$  and  $R_1(c_1/r_1) > 0$ . Direct calculations show that the later condition follows from (4.27) while the former holds for values of  $c_1$  and  $c_2$  that are between the straight lines  $c_2 = c_2^\pm(c_1)$ . This completes the proof of 1(b).

The remaining statements follow reasoning as before. ■

In addition, we can be solving the equations on  $c_{ij}$  (reps.  $c_i$ ) yield conditions for exclusion or conditional tri-stability that depend on the so-called on the com-competition strength of each species (respect Handling time). Before the next explanation, recall that theorem 4.4 prove it that system 4.4 has no equilibrium points in the positive cone, regardless who is the parameter  $c_{ij}$  or  $c_i$ .

**Theorem 4.6.** *Consider system (4.4) and assume that condition (4.26) holds. Then,*

1. *Suppose also that condition (4.27) is fulfilled and*

$$\frac{2}{9} \frac{c_2 r_1^2}{c_1 r_2} < c_{12} < \frac{1}{4} \frac{c_2 r_1^2}{c_1 r_2}, \quad (4.30)$$

*else the curves*

$$c_{21}^\pm(c_{12}) = \frac{1}{27} \frac{c_2 r_1 (9c_1 r_2 c_{12} - 2c_2 r_1^2) \pm 2\sqrt{c_2 (c_2 r_1^2 - 3c_1 r_2 c_{12})^3}}{c_1 c_2 c_{12}^2} \quad (4.31)$$

*on the  $c_{12}c_{21}$  parameter space, that show up from equating to zero  $R_2(0)$ . These curves define a region in the positive cone, see Figure 4.5. Then,*

- (a) *If  $(c_{12}, c_{21})$  lies in between  $c_{21} = c_{21}^\pm(c_{12})$  then there exist three non-trivial equilibrium points  $E_\pm^c, E_3$  in the positive cone. Ordered by its first component,  $E_-^c < E_3^c < E_+^c$ .*
  - (b) *If  $(c_{12}, c_{21})$  does not lie in between  $c_{21} = c_{21}^\pm(c_{12})$  then there exists a single non-trivial equilibrium point  $E_3$  in the positive cone.*
2. *Besides, if condition (4.29) holds, then there exists a single non-trivial equilibrium point  $E_3$  in the positive cone. If condition  $c_{12} = \frac{1}{3} \frac{c_2 r_1^2}{c_1 r_2}$ ,  $c_{21}^\pm$  collide in a single curve. The outcome is also a single positive coexistence equilibrium point.*



**Proof:** Let us consider  $R_2(0) = 0$ , again it is a second order equation of the form  $-b(b_2c_{21}^2 + b_1c_{21} + b_0) = 0$ . Solving such an equation in  $c_{21}$  and arranging terms yields expression (4.31). Note that the most right hand condition (4.30) ensures that the curves (4.31) are well defined, in the sense that the expression under the square root is positive. Coefficient  $b_2$  is positive, so that equation  $R_2(0) = 0$  possesses two positive roots if

$$b_1 < 0 \Leftrightarrow c_{12} > \frac{2c_2r_1^2}{9c_1r^2}$$

and

$$b_0 > 0 \Leftrightarrow c_{12} < \frac{c_2r_1^2}{4c_1r^2}.$$

Summing up,  $c_{12}$  fulfilling (4.30) ensures i) that  $c_{21}^\pm$  are well defined and ii)  $R_2(0)$  is positive if  $c_{21}^-(c_{12}) < c_{21} < c_{21}^+(c_{12})$ . Therefore,  $Seq(0) = \{-, +, ?, +\}$  and  $Seq(r_1/c_1) = \{+, +, +, +\}$ , so that the only way of having three equilibrium points is that  $R_1(0) < 0$ , that is equivalent to:

$$c_{21} > \frac{r_1(7c_1r_2c_{12} - 2c_2r_1^2)}{9c_1c_{12}^2} := \tilde{c}_{21}(c_{12}).$$

Direct calculations show that  $\tilde{c}_{21}(c_{12})$  crosses the  $c_{12}$  axis faraway than  $c_{21}^-(c_{12})$  does and that  $\tilde{c}_{21}(c_{12}) < c_{21}^-(c_{12})$ . Therefore,  $c_{21}^-(c_{12}) < c_{21} < c_{21}^+(c_{12})$  implies  $\tilde{c}_{21}(c_{12}) < c_{21}$ , what completes the proof of 1(b).

The remaining statements follow reasoning as before. ■

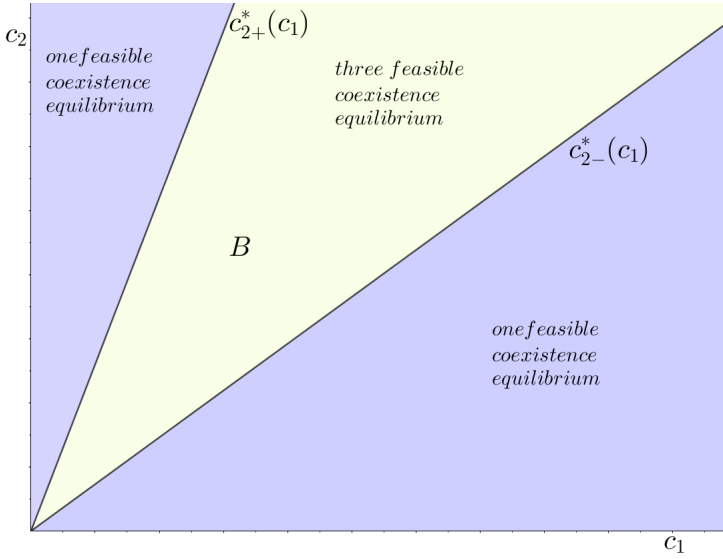
### Stability.

We gather the stability conditions of the equilibrium points found in the previous section in the following theorem.

**Theorem 4.7.** *Consider system (4.4), assuming that  $r_1 > 0$  and  $r_2 > 0$ . Then,*

1. *The origin is always unstable and the semi-trivial equilibrium points are always locally asymptotically stable.*
2. *Assume that condition (4.25),  $c_{12}c_{21} - r_1r_2 > 0$ , holds, so that there are no positive equilibrium points. Then there is a separatrix passing through the origin (that is saddle-node) that separates the basins of attraction of the semi-trivial equilibrium points. Thus, one of the species goes extinct due to priority effects.*
3. *Assume now that conditions (4.29) hold. Then there exists a single coexistence equilibrium point  $E_3^c$ , that is unstable. There exists a separatrix line passing through  $E_3^c$  and the origin that defines the basins of attraction of  $E_1$  and  $E_2$ .*
4. *Finally, if conditions (4.27) and (4.30) hold. Then there exist three non-trivial equilibrium points:  $E_3^c$  is locally asymptotically stable while  $E_\pm^c$  are unstable. There exist separatrices passing through the origin and each of  $E_\pm^c$  that define a region were  $E_3^c$  is located and define the basis of attraction of  $E_1$ ,  $E_2$  and  $E_3^c$ .*

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**Figure 4.4:** Species competition outcomes as function of the intra-species competition  $c_i, i, j = 1, 2$ . The straights  $c_{2\pm}^*(c_1)$  show the thresholds values separating the regions where one or three coexistence equilibria exist in the positive cone, it mean when  $(c_{12}, c_{21}) \notin B$  (blue colored area) or  $(c_{12}, c_{21}) \in B$  (green colored area) that is the region where three equilibria arise. Outside it, just one coexistence equilibrium is possible. The figure is generated with the parameter values  $c_{12} = 0.5, c_{21} = 0.07, r_i = k_i = 1, i = 1, 2$ .

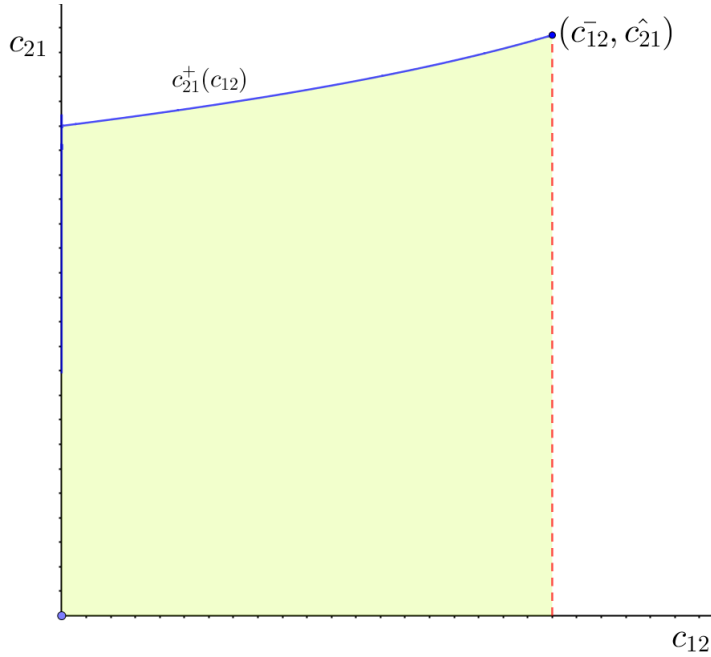
**Proof:**

1. Keeping in mind remark 4.3, consider the nullclines of system (4.4), given by

$$\begin{aligned} f_1 : x_2 &= \frac{1}{a_{12}^2} [r_1\sqrt{x_1} - b_1a_{11}x_1]^2, \\ f_2 : x_1 &= \frac{1}{a_{21}^2} [r_2\sqrt{x_2} - b_2a_{22}x_2]^2, \end{aligned} \tag{4.32}$$

Condition (4.25) imply that the nullclines (4.32) divide the positive cone in three different regions, as displayed in the left panel of figure 4.6. Region I is characterized for  $x_1' < 0$  and  $x_2' > 0$ , and the flow points inward on the boundary of region I, so that it is a trapping region and solutions starting within the closure of region I are attracted by  $E_2$ . So that the origin is unstable. Reasoning as before we get that region III is a trapping region and any solution starting within the closure of region III is attracted by  $E_1$ . It is immediate that  $E_1$  and  $E_2$  are locally asymptotically stable just by considering the flow of the system on the straight lines given by  $\{(z_1, v_{2z_2}), z_1 \geq v_{2z_1}\}$  and  $\{(v_{1z_1}, z_2), z_2 \geq v_{1z_2}\}$  respectively, where  $(v_{1z_k}, v_{2z_k})$  are the coordinates of the vertex of the nullcline of  $z_k, k = 1, 2$ .

2. Considering for a while that there is perfectly symmetric competition, that is to say that  $c_{12} = c_{21}, c_1 = c_2$  and  $r_1 = r_2$ . Then, the geometry of the phase portrait yields that the straight line  $z_2 = z_1$  is the *stable manifold* (a forward invariant curve such that solutions starting on this line converge to the origin). Besides, divides the positive cone on the basins of attraction of the semi-trivial equilibrium points. Furthermore, because of the continuity of the flow with respect to the system parameter and the uniqueness of



**Figure 4.5:** Species competition outcomes as function of the competitive strength  $c_{ij}, i, j = 1, 2$ . The axes, the curve  $c_{21}^+(c_{12})$  and vertical line  $\bar{c}_{12} = \frac{1}{4} \frac{c_2}{c_1} \frac{r_1^2}{r_2}$  show the thresholds values separating the regions where one or three coexistence equilibria exist in the positive cone. Outside it, just one coexistence equilibrium is possible. The figure is generated with the parameter values  $c_1 = 1, c_2 = 1, r_i = 8, i = 1, 2$ .

solutions on the positive cone, this invariant manifold changes continuously as the model parameters change as long as no positive equilibrium points appear in the positive cone.

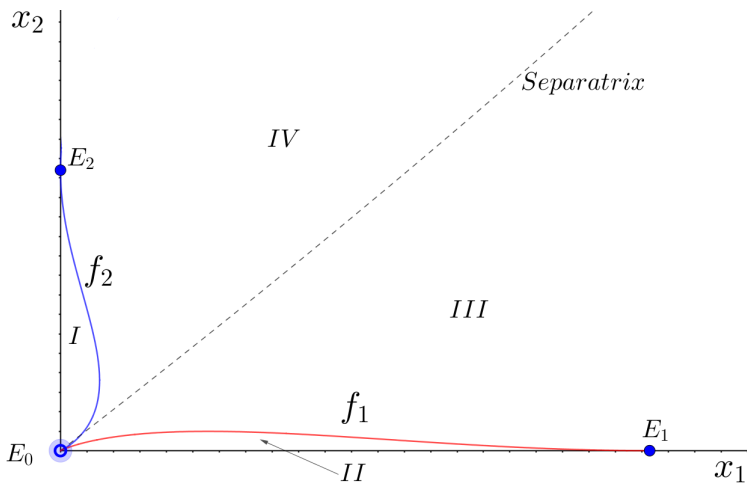
3. This proof is an adaptation of that of Theorem 4.2, item 2.a in [20]. Consider, as before, the perfectly symmetric case. Then the geometry of the phase plane ensures that  $E_3$  is a saddle-node and that the straight line  $z_2 = z_1$  is its stable manifold that defines the basins of attraction of the semi-trivial equilibrium points. As argued before, this settings remain qualitatively the same as the coefficients of the system vary continuously whenever no additional equilibrium points show up in the positive cone.
4. It follows *mutatis mutandi* the previous one (see also the proof of Theorem 4.2, statement 2.a in [20]).

■

## 4.4 Discussion and conclusions.

We next revisit the mathematical results from a biological point of view taking into account the aims stated in the introductory section. We also compare our model with the classical model, note that even if straight comparisons with the classical model are not possible (see the Introduction section of this chapter), we can do so from a qualitative point of view. Thus, we leave assessing similarities and differences with Holling type II and IV competition models to the

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**Figure 4.6:** Left panel: The phases portrait for the interactions' populations competition. The figure is generated with the parameter values  $a_{12} = 0.84$ ,  $a_{21} = 1.10$ ,  $a_{11} = 0.99$ ,  $a_{22} = 0.75$ ,  $K_1 = 0.95$ ,  $K_2 = 0.90$ ,  $r_i = 1$ ,  $i = 1, 2$ .

general conclusions chapter 5.

A first claim is that competition outcomes are different. The classical model allows for three possible outcomes: i) global (or unconditional) species coexistence, ii) one (unconditional) species exclusion and iii) competitive exclusion due to priority effects. Interestingly, instead, the sessile competition population model only allows for: i) tri-stable conditional coexistence and ii) competitive exclusion due to priority effects.

Therefore, the sessile model does not allow for "super competitors", i.e., those that will exclude the other species *regardless* of initial conditions.

A second claim is that global coexistence is not allowed by system (4.4). This feature is interesting from management point of view, whenever species coexist, a sufficiently strong variation in the number of individuals of one of the species may broke such an state and lead one of the species to extinction. On the other side, reinforcing an species (for instance, reforestation) increasing its population size may revert push species to either coexist or even revert the competitive outcome.

We next analyze in deeper detail these features.

### 4.4.1 Sessile vs mobile species competition

Theorem 4.3 concerns a mobile population 1 competing a sessile population 2. This Theorem tells us that the outcomes of this model are the same as in the classical model plus bi-stable conditional coexistence in favor of species 2, the sessile species. The last dynamical outcome has already been observed in [20, 21] when modifying the classical competition model with Holling type II and IV competitive responses. Also in [1, 64] when considering social (herd) behavior in one of the competing species.

The structure of the regions in the parameter space  $a_{12}a_{21}$  leading to each outcome (see figure 4.2) are equivalent to that of the classical model except for the bi-stable conditional coexistence in favor of species 2 region. This region is set in the region where the classical model predicts that species 1 would be excluded by species 2, and borders the species exclusion due to priority effects and (partially) the global coexistence regions. Therefore, in such a region species 2 can not be ruled out by species 1 but both species may coexist provided an appropriate initial amount of individuals of each species. Thus, coexistence is more likely than in the classical model.

Interestingly, consider inter species competition coefficients  $(\hat{c}_{12}, c_{21})$  that are set in the region where species 2 wins. Fixed  $\hat{c}_{12}$ , as  $c_{21} < \phi_{b_2}(\hat{c}_{12})$  the effect of species 1 on species 2, increases and crosses the curve  $c_{21} = \phi_{b_2}(\hat{c}_{12})$ , species 1 has a chance for survive via coexisting with species 2. A further increment such that  $c_{21} > 1$  makes the effect of species 1 on species 2 strong enough so that in the end there can be only one species.

In the overall being sessile seems not to be harmful for this species, since they will survive the same as if it were mobile. On the contrary, it is beneficial to the mobile competing population, since they have more chances of survival.

#### 4.4.2 The intra and inter-species competition effect for nullclines.

We first analyze qualitatively the nullclines of system (4.4) to the nullclines of the classical competition model (4.1)). Let as note an important fact that concerns both intra and inter species competition coefficients. These coefficients are somehow non comparable since they are expressed in different units (in the classical/sessile population models). Therefore, even if we plot both nullclines in the same axes, as in figure 4.7, we do not know how these parameters vary together. Keeping that in mind, we focus on the  $x_1$  nullclines given by

$$x_2 = f_1(x_1) = \frac{1}{a_{12}}(\hat{r}_1 - a_{11}x_1) \quad x_2 = \hat{f}_1(x_1) = \frac{x_1}{d_1^2 \hat{a}_{12}^2}(\hat{r}_1 - b_1 \hat{a}_{11} \sqrt{x_1})^2 \quad (4.33)$$

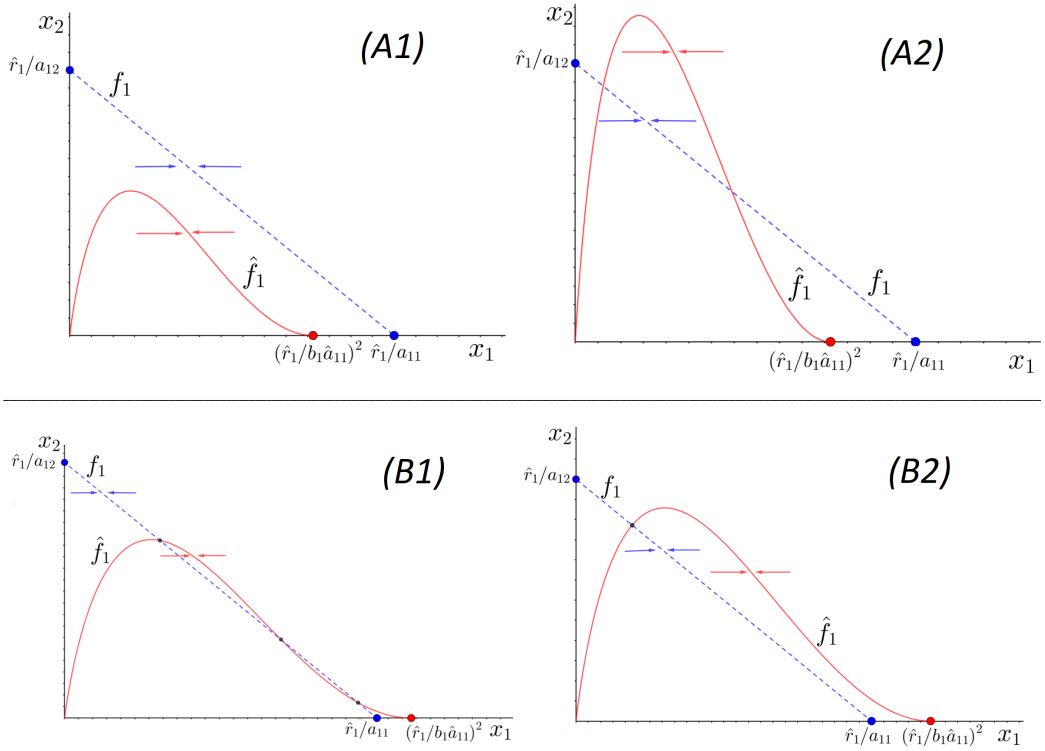
As mentioned early the nullcline of species 1 defines the values of population size of species 2 that allow species 1 to keep growing. For instance, the  $f_1$  nullcline of the classical model is a straight line with negative slope (see figure 4.7, blue dotted straight line) which means that the larger is  $x_1$  the less tolerant is to the presence of  $x_2$ . In other words, it means that  $x_1$  continues growing only if  $x_2$  decreases.

Figure 4.7 represents the possible relative positions of the  $x_1$  nullcline in the classical and sessile populations models.

A first claim is that at low  $x_1$  population size the sessile model is highly tolerant to an increase in the number of individuals of both species 1 and species 2. This feature, that is at odds with the classical model, can be explained paying attention at the peculiarities of the sessile model since interactions take place at the boundary of either the vital surroundings of each individual (intra species) or the region occupied by each population (inter species). On the one hand, at low population size intra species competition does not play a major role as the population grows, since individuals only interact with the nearby ones and there are only few of them. At the same time, inter species interactions take place only at the boundary of the area occupied by species 1. Thus, population growth is the main driver of population dynamics at low densities. This trend is maintained at low densities, while  $\hat{f}_1$  is increasing. Direct calculations

yield that the maximum of  $\hat{f}_1 \hat{x}_2 := \frac{1}{4^2} \frac{r_1^4}{b_1^2 a_{11}^2 a_{12}^2}$  is reached at  $\hat{x}_1 := \frac{1}{4} \left( \frac{r_1}{b_1 a_{11}} \right)^2$ .

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**Figure 4.7:** The nullclines  $x'_1 = 0$  of systems (4.4) and classical model (4.1).

A second claim is that from  $\hat{x}_1$  on the nullcline decreases, meaning that if  $x_1$  increases slightly (so that intra species competition pressure increases), species 1 can keep growing only if species 2 lowers its number of individuals (i.e., reducing the inter species competition pressure). That is, the trend is similar to that of the classical model,

A third feature is that nullclines  $\hat{f}_1$  and  $f_1$  may not cross the horizontal axis at the same point. Indeed, the crossing points can be ordered in any way (see figure 4.7).

Finally, note that both nullclines can meet essentially in four different ways, as in figure 4.7. Let us interpret one of them, for instance panel (A1). In the region below  $\hat{f}_1$  (above  $f_1$ )  $x_1$  increases (decreases) in both models. On the contrary, in the region between  $\hat{f}_1$  and  $f_1$  species 1 would keep growing if represented by the classical model but would decrease if represented by the sessile populations model.

Note that the maximum of  $\hat{f}_1$  can be below (panel (A1)) or above (panel (A2))  $f_1$ .

### 4.4.3 The intra and inter-species interaction and coexistence equilibria.

Finally, we examine competition outcomes taking into account intra and inter-species competition, that yield conditions for species exclusion due to priority effects or conditional tri-stability.

We may let vary either the intra-species competition parameters  $c_i$  for fixed values of the inter species competition parameters  $c_{ij}$  or the way round. Note that coefficient  $c_i$  is a conglomerate

erate of different factors that include intra-specific interaction  $a_{ii}$  and  $b_i$ , the relation between the perimeter of both the "vital space" around each individual and the perimeter of the area occupied by the whole population.

### Varying intra species competition coefficients for fixed values of inter species competition coefficients

Theorem 4.5, that tells us that under conditions (4.26) and (4.27) two possible outcomes are possible: either both species can coexist via tri-stable conditional coexistence or one of them goes extinct via priority effects.

In particular,  $(c_{11}, c_{22})$  lying between  $c_{22} = c_{22}^{\pm}(c_{11})$  (the straight lines defined in (4.28)) then there is tri-stable coexistence. Thus, consider fixed values of  $c_{ij}$  and  $r_i$  fulfilling the hypotheses of Theorem 4.5. Then, for each fixed value  $c_2^*$ :

- There is species coexistence via conditional tri-stability for  $c_{11} \in (c_{11}^-, c_{11}^+)$  where  $c_{22}^* = c_{22}^+(c_{11}^-)$  and  $c_{22}^* = c_{22}^-(c_{11}^+)$ .
- There is one species exclusion due to priority effects if  $c_{11} \notin (c_{11}^-, c_{11}^+)$ .

Everything works symmetrically if  $c_{11}$  is fixed and  $c_2$  let to vary. We may conclude that for each value of  $c_{ii}$  coexistence is possible for moderate values of  $c_{jj}$ ,  $i \neq j$ . However, either low or large enough values of  $c_{ii}$  or  $c_{jj}$  would broke coexistence.

Consistently with the classical model, numerical experiments show that the basins of attraction of  $E_1$  is larger than the basin of attraction of  $E_2$  for  $c_{11} < c_{11}^-$ . The result is reversed as  $c_{11} > c_{11}^+$ . This feature strongly suggests that the trade-off between intra and inter species competition forces works different in sessile populations than in mobile populations.

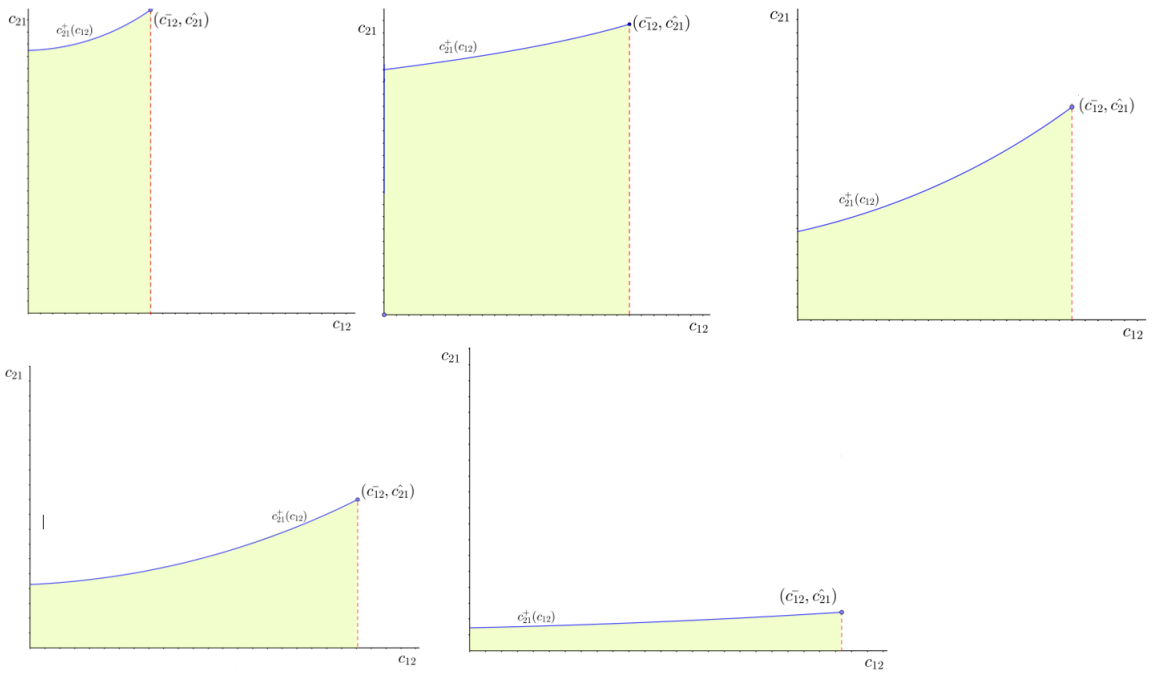
### Inter-species competition

We fix now  $c_{ii} > 0$  for  $i = 1, 2$  and assume that condition (4.30) in Theorem 4.6 holds. Then, in a similar way as in the previous paragraph, there are conditions on the coefficients of the model that lead to either coexistence via conditional tri-stability or species exclusion due to priority effects. In contrast, the curves defining the combination of inter species competition coefficients leading to each outcome are nor straight lines and define a closed region on the positive cone, see figure 4.8. Inside such a region there is conditional conditional coexistence while outside the Competitive exclusion principle rules species competition. Note that the shape of such a region changes as the other parameters change (in this case  $c_{22}$  changes as shown in the caption of figure 4.8). Note that the tri-stability region starts dropping towards the axis  $c_{12}$  as  $c_{22}$  increases.

This viewpoint (fixing  $c_{ii}$  and varying  $c_{ij}$ ) is consistent with the classical model, meaning that a pair  $(c_{12}, c_{21})$  close to the horizontal  $c_{12}$ -axis (i.e.,  $c_{12} > c_{21}$ ) makes the basin of attraction of  $E_2$  larger than that of  $E_1$  and conversely.

As when we fixed  $c_{ii}$ , it seems that moderate values of  $c_{ij}$  promote species coexistence.

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**Figure 4.8:** Competition outcomes of system (4.4) as function of the inter-species competitive interaction  $c_{12}$ ,  $c_{21}$  for a fixed value of  $c_{11}$  and increasing values of  $c_{22}$ . The figure is based analytic expression depending of condition case on numerical calculations and has been edited to improve it. Parameter numerically fixed values  $r_1 = 7.5$ ,  $r_2 = 8$   $c_{11} = 0.9$  and of  $c_{22} = 0.3, 1.1, 2.75, 3.3,$  and  $16.7$ .



# General conclusions and future research lines

This section is intended to compare all the three models presented herein. Thus, we shall point out both common trends and main differences. A detailed analysis of each model has been performed at the end of the corresponding chapter.

A first and important claim concerns both intra and inter species competition coefficients. These coefficients are expressed in the same units,  $1/(time \times individuals)$ , in the models with Holling type II and IV competitive response but units are different in the sessile populations model:  $1/(time \times \sqrt{individuals})$  and  $1/time$  for intra and inter species competition, respectively. Anyway, even if units are different, we may compare nullclines from a qualitative point of view as well as compare the structure of each model's possible outcomes with respect to inter species competition coefficients.

All the models arise from paying attention to the way interactions take place. However, we may group the models into two different categories. On the one hand the Holling II and IV type models are straight extensions of the classical model, meaning that making coefficient  $c_i = 0$  (Holling type II model) or  $g_i$  (Holling type IV model),  $i = 1, 2$  yields the classical model. On the other hand, the sessile population model is a reinterpretation or contextualization rather than an extension of the classical model.

In the overall, we have fulfilled the aims stated at the introduction (see section 1.3) since:

- Holling type II and IV competitive responses reflect the fact that competition may not be instantaneous.
- We derive equation systems to model realistic mechanism/settings such that the per capita growth is not linear.
- The sessile population model is suitable for an extreme case of non well mixed populations: those whose individuals do not move.

For the sake of simplicity, we follow the common structure of each chapter conclusions' section. Thus, we first compare the effect of the different mechanisms on the nullclines of each

model. Then, we compare the possible outcomes of each model and its structure with respect to the parameters of the model. We do so when the mechanism affects only one of the competing species and when both of them exhibit the corresponding feature.

### 5.1 Nullclines analysis

Nullclines are the zero growth curves of the corresponding differential equations system. Figure 5.1 displays the nullcline  $f_1$  of species 1 in the classical model along with those of the new models presented herein. Let us recall that the region below  $f_1$  consists of the pairs  $(x_1, x_2)$  such that  $x_1' > 0$ . In words, the populations sizes that allow species 1 to keep growing, that is to say, its crown tolerance [94].

Note that the  $x_1$  nullcline of all the three new models can exhibit a maximum that is not present in the classical model (see solid lines in Figure 5.1). That is to say that there are settings (combinations of parameter values) that allow species 1 to keep growing in the presence of an increasing amount of competitors up to certain extent. Even if no maximum is achieved (see dotted lines in the top row panels in figure 5.1) in the Holling II and IV models, the area below  $f_1$  is larger than in the classical model. That is to say the species 1 keeps growing where the classical model predicts the contrary. This feature is enabled by the competitive responses, that relax inter species competitive pressure with respect to the classical model. This last feature seems to be inherent to any species competition model with non linear per capita growth [7], [20], [21], [64], [72] (to cite few references). From a geometrical point of view, it is due to the curvature of the nullclines [72, 83].

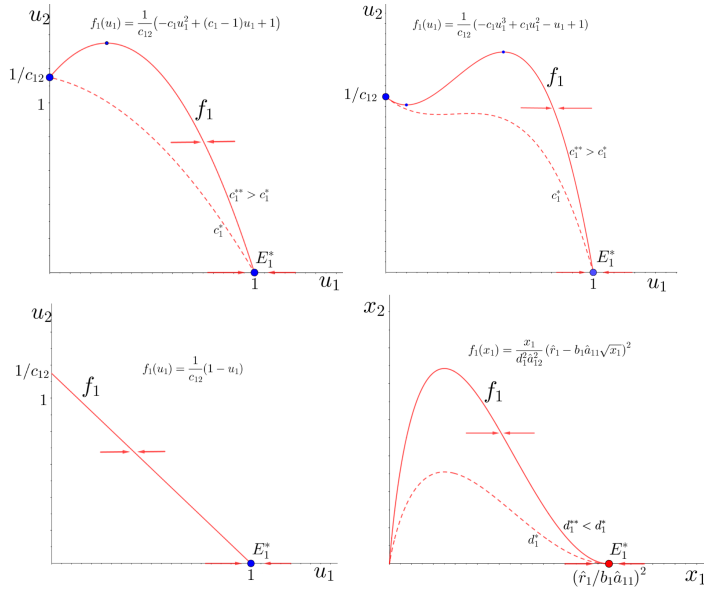
From a different point of view, the classical model can be seen as a limit case of instantaneous interference [20] or no group defense [21].

The nullcline  $f_1$  corresponding to the Holling type II and IV models meets the axes at the same points as in the classical model [69]. the curvature of the nullclines of the Holling type II and IV models makes that the region below the nullcline to be larger than for the classical model. Thus, species 1 species 1 can keep growing in the presence of larger amount of individuals of species 2 that in the classical model. Interestingly, even if the effect of group defense is low (dotted curve in the top right panel of figure 5.1) it always is better that nothing. Therefore, in absence of other strategy, making the competitor waste time or grouping for defense purposes increases the chances of keep growing for species 1.

In contrast with Holling type models, at low  $x_1$  population size (close to zero) the sessile model nullcline is always increasing. Note that in this model inter competition takes place at the boundary and intra species competition is only with close neighbors, so that higher crown tolerance is expected.

### 5.2 Dynamical outcomes

In this section we pay attention to the possible competition outcomes, that we have summarized in figures 5.2, 5.4 and 5.5. A common feature is that all the three new models allow for bi conditional coexistence in favor of species  $i$  and tri-stable conditional coexistence. Let us recall that the former allows for species coexistence or species  $j$  extinction, and what outcome actually occurs depends on priority effects. Besides, in the tri-stable conditional coexistence scenario species coexistence as well as one (or the other one) species extinction due to priority is possible. The classical model exhibits no transitions between regions, meaning that a subtle



**Figure 5.1:** Nullcline  $f_1$  of population 1 in the the competition model with Holling type II (left) and Holling type IV (center) competitive response, respectively. The right panel stands for the sessile competition model. Doted curves represent alternative

change around 1 in, lets say,  $c_{12}$  changes from species coexistence to species 1 exclusion. Thus, the above mentioned new outcomes are a kind of nuances or "gradient" scenarios allowing for intermediate, not so dramatic, outcomes.

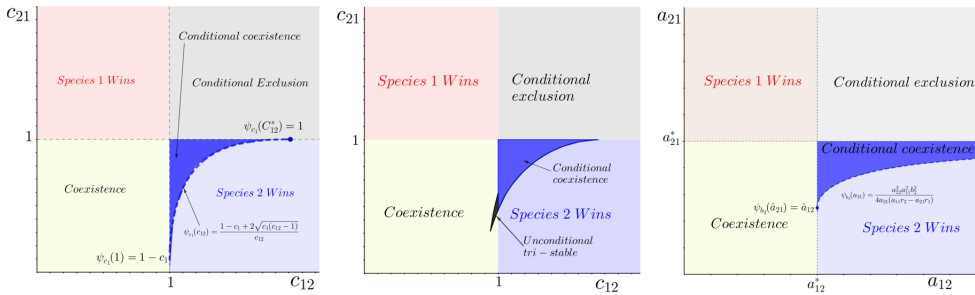
As pointed out in the introduction, the classical model is a particular case of the Holling II and IV type competitive models. Thus, it is not surprising that the later models exhibit all those outcomes allowed by the classical model, i.e., unconditional global coexistence, one species unconditional exclusion and one species exclusion due to priority effects. On the contrary, the sessile population model does not allow for global coexistence nor one species unconditional exclusion, as it is in the wave of competition models with social behavior [10], [46], [64]. Interestingly, if just one of the competing species can move global coexistence and one species unconditional exclusion are among the possible competition outcomes (see Theorem 4.3 and figure 5.2). It strongly suggests that these outcomes are linked to mobile populations.

### 5.2.1 Classical vs new species behavior in a single species

We next compare the effect of the exhibiting competitive response/sessile condition on a single population. A common feature of all the three models is that enable species coexistence via bi-stable conditional coexistence. Competitive response is exhibited by species 1 as in systems (2.5) and (3.5) and doing so benefits species 1, while species 2 is the motionless one in the sessile model (which benefits species 1). Thus, doing so we enable a comparison (as fair as possible).

Imagine that species 1 can choose one among two strategies:

## 5. General conclusions and future research lines



**Figure 5.2:** Competition outcomes of the competitive response/sessile condition on a single population for systems (2.5) in left panel, (3.5) central panel and (4.9) right panel. Code color: green for global coexistence, gray for competitive exclusion, light red for species 2 exclusion, dark red for bi stable conditional coexistence in favor of species 1, light purple for species 1 exclusion and dark blue region represents bi stable conditional coexistence in favor of species 2.

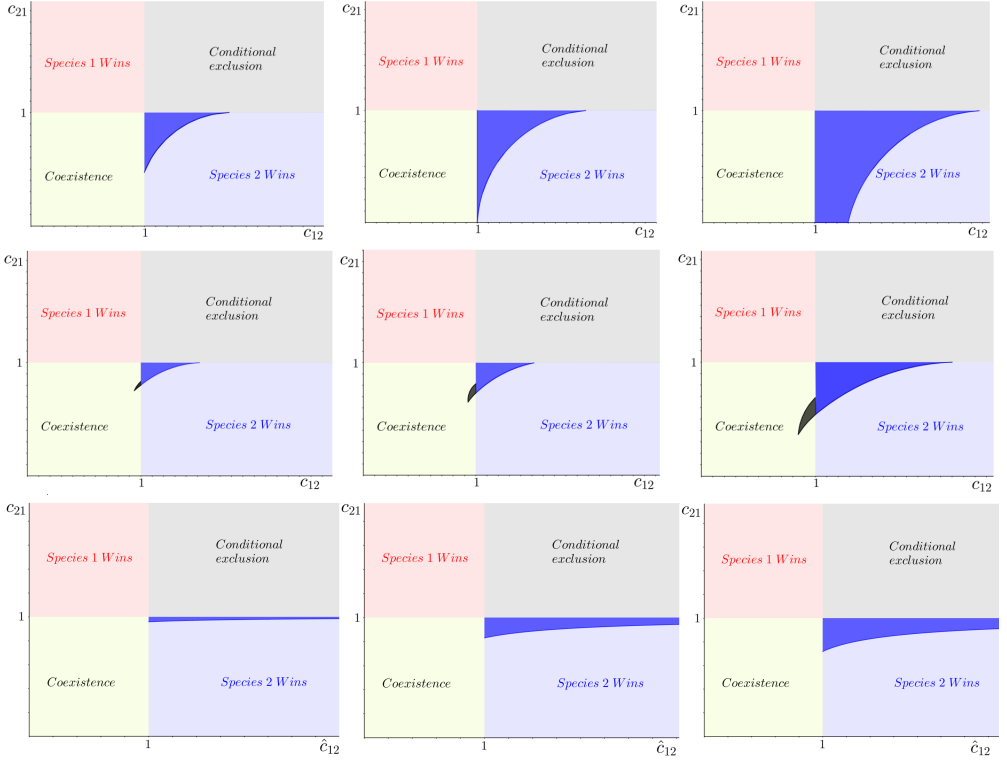
1. Make the competitor waste more time in competition (instead of straightly running away) as in Holling II type response.
2. Group somehow to defend themselves from competitors as in Holling IV type response.

Both strategies give chance to species 1 of coexist when the classical model predicts its extinction. An interesting question is what is the best strategy in terms of which one yields a larger range of parameter values allowing species 1 to survive. We have computed in figure 5.3 the dynamical outcomes of the competition model with Holling II type (top row) and Holling IV type (second row) competitive response for different values of the competitive strength (the same in both models) and values of the parameters  $c_1$  (related to time spent competing) and  $g_1$  (related to group defense) lower, equal and larger than the threshold value 1. It is apparent that making species 2 waste time in competition is by far more beneficial to species 1 than grouping for defense purposes. It is likely due to the fact that in the first strategy all the individuals contribute to "face" competitors while grouping dilutes this effect.

For its part, in the sessile population model the bi-stable conditional coexistence region increases as  $b_2$  increases. This coefficient is not easy to interpret: it is the ratio of the perimeter of the *vital space* circle around each individual to the perimeter of the region occupied by this population. Thus, the mobile is more like to survive as the vital space of the sessile population individuals is larger, which means having less individuals around. Thus, having lower intra-species pressure compered to inter-species pressure. Note that the values of  $b_2$  used in figure 5.3 are far from realistic. We have chosen these ones so the the effect could be visible.

### 5.2.2 Classical vs new species behavior in both species

In the overall, models with Holling II and IV competitive response obviously expand the possible outcomes of the classical competition model, see figure 5.4. As pointed out above, the new outcomes and its corresponding regions in the parameter space  $c_{12}c_{21}$  are a kind of gradient between the more drastic transitions between classical outcomes. On the other hand, the sessile model belongs to a different class of models (those with social structure). This models allows only two dynamical outcomes: tri-stable conditional coexistence and competitive exclusion. Parameters are different from the Holling type II and IV, but it is clear that the regions of global coexistence and global one species exclusion are not possible in this model. Anyway,



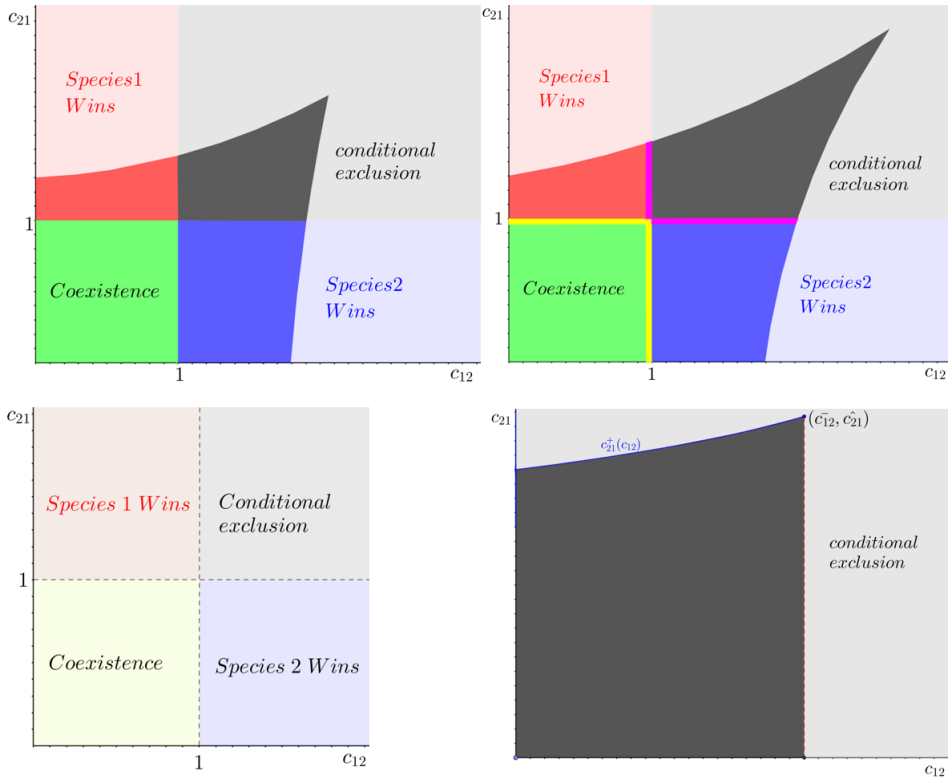
**Figure 5.3:** Numerical simulation for systems (2.5) (first row) and (3.5) (second row), where species 1 exhibits competitive response (type II in top row, type IV in bottom row) while species 2 does not. The third row concerns the sessile populations system (4.9), where species 1 is mobile while species 2 is sessile. The code color is the same as in figure 1.1: green for global coexistence, gray for competitive exclusion, red for species 2 exclusion, purple for species 1 exclusion; the new dark blue region represents bi-stable conditional coexistence in favor of species 1 and the black region (right panel) represents tri-stable unconditional coexistence. The figure is based on numerical calculations (the code is available in [19]) and has been edited to improve it. Intrinsic growth rates  $r_i$  are fixed and the same in all the panels. Parameters  $c_{12}$ ,  $c_{21}$  range in  $[0, 2]$ , and coefficients  $c_1 = g_1 = 0.75$  (left column),  $c_1 = g_1 = 1$  (center column) and  $c_1 = g_1 = 2.75$  (right column). Note that  $b_2$  in system (4.9) is not comparable to  $b_1$  and  $g_1$ ; from left to right  $b_2 = 0.4, 0.75, 0.9$ .

the basin of attraction of the semi-trivial equilibrium points are somehow consistent with the classical model meaning that, for instance, the basin of attraction of  $E_2$  is larger for values of  $(c_{12}, c_{21})$  close to the  $c_{12}$  axis.

A common trend is that either the larger is the time spent in competition (Holling type II), stronger is the group defense effect (Holling type IV), or the larger are the intra species competition coefficients  $a_{ii}$  (sessile populations) the wider is the tri-stable conditional coexistence region in all the three new models. Interestingly, this feature is in consonance with the classical thoughts [83, 94]. The peak form of the tri-stable conditional coexistence regions implies that for larger values of the competitive strengths (Holling II and IV models) or inter species competition pressure (sessile model) coexistence is more unusual. Moreover, in this region slight changes in the competitive coefficients may break coexistence into competitive exclusion. Note that we have assumed that the effect increases more or less the same in both populations; an

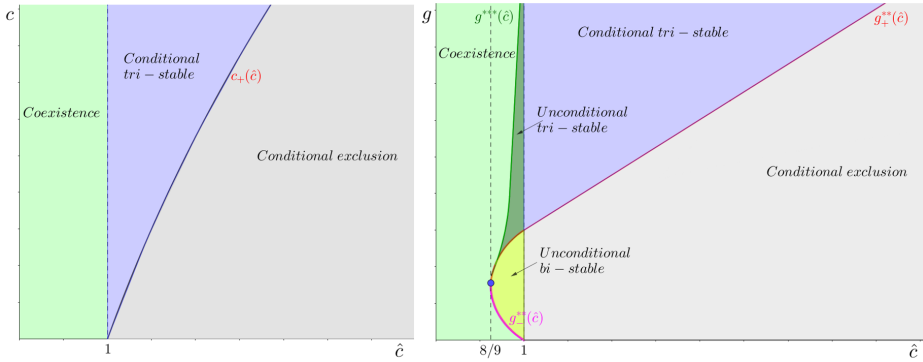
## 5. General conclusions and future research lines

unbalanced growth may pull the peak towards one or the other axis.



**Figure 5.4:** Competition outcomes. Left panels: numerical simulation trends of systems (2.4) and (3.4) as function of competitive strengths  $c_{ij}$ ,  $i, j = 1, 2$  depending of parameter values. All lights Green, red, blue and dark represent classical outcomes of the departures model; dark color represent the new outcomes for of systems (2.4) and (3.4), that correspond to bi-stable, tri-stable unconditional and conditional coexistence. Right panel: analytical outcomes of system (4.4). dark black represent tri-stable conditional coexistence and light black conditional exclusion.

It is also apparent that group defense allows for a broader variety of dynamical outcomes than the Holling type II mechanism (compare sections 2.5 and 3.5. For instance, see figure 5.5 under symmetric competition or section 3.5.3; in this case  $c_{12} = c_{21}$  so that the possible outcomes are those in the bisectrix of the positive cone (see top left panel - Holling type II- and top right panel -Holling type IV- in figure 5.4). However, still in the symmetric case, it is not clear whether Holling type II (figure 5.5 left panel) or IV (figure 5.5, right panel) competitive response makes a true difference, meaning that the global coexistence step is the same, and the competitive exclusion and conditional tri-stable coexistence regions are not so qualitatively different. Fixed a value of  $\hat{c}$ , Holling II type model needs of a larger value of  $c$  to achieve the tri-stable conditional coexistence region, see figure 5.5. A general expression computing the area below curves  $g_+$  and  $g_+^{**}$  can be easily computed, although its expression is quite complicated as depends on many parameters.



**Figure 5.5:** Competition outcomes of systems (2.4) (Holling type II, left panel) and (3.4) (Holling type IV, right panel) under symmetric competition. The horizontal axis  $\hat{c}$  represents the ability of each species to limit the effect of the other one (by making waste time -left- and due to group defense -right-) and the vertical axis represents the competitive strength. Curves  $g_+$ ,  $g_+^{**}$  and  $g_+^*$  are defined in (2.22), (3.12) and (3.14), respectively. Color code: green, dark green and yellow represents global coexistence, bi-stable and tri-stable unconditional coexistence, respectively, while blue and light black represents the conditional coexistence and the competitive exclusion regions, respectively.

Interestingly, the unconditional bi and tri-stable coexistence outcomes may help in explaining competing species that may coexist through two alternative coexistence states [36].

### 5.3 Future research

The results presented herein fulfill the initial research questions stated, but are not a dead end street. Indeed, open the door to future research. We next briefly sketch ideas for future research lines:

1. **More on competitive responses:** there exist at least 20 different functional responses, each of them addressing peculiar population features. An obvious way to carry on this research is analyze which ones admit translation to the species competition context.
2. **Eco-epidemic competition models:** Eco-epidemics, term coined by O. Arino [Arino1999], is currently a vibrant research field concerned with the interplay between diseases and population dynamics [8, 10, 38]; sadly, while writing these lines the unknown impact of COVID-19 is a hot issue.

The models set up in this dissertation expand the classical competition model and it is of full interest understanding how competitive responses or sessile competing populations perform when facing different diseases.

3. **Competition in patchy environments** Patchy models allow to incorporate spatial heterogeneity as well as to model fragmented landscapes or ecosystems. There are lot of works on spatially distributed competition models [Amarasekare2001, Amarasekare2004, Bravo2010, Marva2015], but all of them consider the classical competition model. From the perspective of species conservation ecology and ecosystems management there are two main tools related to species dispersal: ecological corridors [Revilla2008], [Franco2015] and creating artificial refuges [Brochier2015, Reading1997, Watanuki2006].

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Again, an interesting question is ascertain whether more realistic spatially competition models work different from the classical models.

4. **Periodic competition models** Many physic parameters that describe environmental conditions (light, temperature,...) change in time and many often in a periodic way. Such a variations have a huge impact on populations living therein: feeding, matching, large migrations or activity level, to cite few of them. Periodic (non-autonomus) ODE systems are suitable tools to incorporate such a periodically changing environmental conditions to population models. Again the main aim consists of extending the classical periodic interference competition model by adding different competitive responses or considering periodic the corresponding sessile populations competition model.
5. **Data analysis** There are many experimental works on species competition whose data that display competitive response, but no explicit form has been found. Thus, we intend to analyze whether one of the models presented herein fit well a given data set or whether a different competitive response term (to be set) works better.

This aim will need of collaborating with research other team that either has already collected data or is able to run experiments to collect that data.



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