



MATHEMATICAL MODELLING
IN ENGINEERING & HUMAN
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Preface

This book includes the extended abstracts presented at XXV Edition of the Mathematical Modelling Conference Series at the Institute for Multidisciplinary Mathematics Mathematical Modelling in Engineering & Human Behaviour.

December 2023

Juan Ramón Torregrosa
MME&HB 2023
Universitat Politècnica de València

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Modeling interference on interference competition models

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Abstract. Paradoxically, prior interference competition models did not account for the effect of both intra- and inter-species interference. We do so by adapting the works of Beddington [2] and DeAngelis [7] on predator-prey models to the classical Gause interference competition model [8]. The established theory states that global species coexistence (i.e., regardless of the initial amount of individuals) is only possible, roughly, when the ratio of the inter-species effects over the intra-species effects is less than 1. This feature was intended to support the Gause’s Competitive Exclusion Principle (two species competing for the same resource can not -hardly- coexist) and the Coexistence Paradox (this hypothesis is at odds with Nature). We have found that taking into account intra-species interference in competition allows competing species to global coexistence even if the above mentioned ratio is larger than 1. This feature was not allowed in previous works on interference competition that introduced herd-type behavior [1], [3], [13], the time spent in competition [4] or group defense [5]. We have also found multi-stability scenarios not allowed by the classical model [8] but found in the above mentioned references which, in turn, here are feasible in a wider range of the parameters space due exclusively to intra-species interference when competing heterospecifics. Therefore, accounting for interference contributes to unveil the Paradox of coexistence.

Keywords: interference competition, interfering time, species competition

1 Introduction

The Competitive Exclusion Principle [9] states, roughly, that two species that compete for the same resource can not coexist. Two classical works support this Principle: the Gause [8] (Lotka-Volterra like) competition model was derived for ordinary differential equations based on laboratory experiments with *Paramecium*. The Leslie-Gower difference equations competition model [12] was inspired on the famous experiments with *Tribolium* carried out by Park and collaborators.

Both models share a handful of features. Let $x_i(t)$ be the number of individuals of species $i = 1, 2$ at time t . The Gause model reads as

$$x'_i(t) = r_i x_i(t) - a_{ii} x_i^2(t) - a_{ij} x_i(t) x_j(t), \quad (1)$$

while the Lelie-Gower model is

$$x_i(t+1) = \frac{r_i x_i(t)}{1 + a_{ii} x_i(t) + a_{ij} x_j(t)}, \quad (2)$$

where r_i stands for the intrinsic growth rate, a_{ii} for the intra-species competition coefficient, while a_{ij} measures the competitive effect of species j on species i .

The nullclines of both models are straight lines. Also, assuming that the trivial equilibrium point $E_0^* = (0, 0)$ is unstable, both models allow for four different competition outcomes: either species 1 or species 2 wins regardless of the initial values, global coexistence, or priority effects: one species will go extinct depending on the initial amount of individuals. Interestingly, the competition outcome depends essentially¹ on the same combination of parameters

$$\text{Gause: } \frac{a_{ij} r_j}{a_{jj} r_i}, \quad \text{Leslie-Gower: } \frac{a_{ij} r_j - 1}{a_{jj} r_i - 1}. \quad (3)$$

The above expressions, that we denote indistinctly by c_{ij} , are interpreted as follows: *forget for a moment* of the r 's ratio. Coefficient $c_{ij} < 1$ means that the effect of species j on species i is softer than the effect of species j on species j . Recall that species j would survive in the absence of species i . Thus, $c_{ij} < 1$ means that species j can not drive species i to extinct. Note that condition $a_{ij}/a_{jj} < 1$ can be reversed by multiplying by the ratio of the intrinsic growth rates, i.e., being not harmful enough can be compensated by a sufficiently larger reproduction rate, which must be taken into account [11].

The outcomes of both the Gause (1) and the Leslie-Gower model (2) are summarized in Figure 1 in terms of the above defined c_{ij} , $i \neq j$ coefficients, the so-called *competitive strengths* [4]. In terms of c_{ij} , coexistence or extinction depends on the balance between intra- and inter-species competition [14], [15].

Coexistence seems to be much more common in Nature than species exclusion, which is at odds with the Competitive Exclusion Principle and gives rise to the Paradox of Coexistence. Ecologist have done many work to explain this contradiction (find a recent review in [4]). However, from the deterministic models viewpoint not too much work has been done apart from the recent works assuming herd behavior [1], [3], [13], accounting for the time spent on inter-species competition (individuals interference) [4], and group defense [5].

In this work we set a model that accounts for intra-species interference in competing species in Section 2. Then we summarize the possible outcomes of the model in Section 3 and briefly discuss the results in Section 4.

¹ If λ_i are the eigenvalues of the Jacobian at an equilibrium point E^* , it is asymptotically stable if $\lambda_i < 0$ ($|\lambda_i| < 1$, resp.) for differential equations (difference equations, resp.)

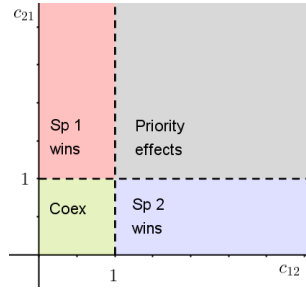


Fig. 1: Outcomes of the classical competition model (1) as function of the competitive strengths c_{12} and c_{21} .

2 The model

Beddington [2] and DeAngelis [7] modeled the effect of interference between predators when hunting preys. This effect can be easily adapted to competing species.

Let us make a comment to clarify the effect we are accounting for. Note that we deal with interference competition (also known as contest competition) which means that, in contrast to exploitative (or scramble) competition, after disputing for a resource one of the competitors will take the whole resource they are competing for. Two heterospecifics may compete for a resource, and the effect of the resulting interference was addressed in [4]. Instead, here, we account for the mutual interference between conspecifics that compete for a resource with a heterospecific. This effect is different from that due to logistic behavior, i.e., that of two individuals of the same species competing for a resource in the absence of an individual of the other species.

The complete competition interference model reads as follows

$$x'_i = r_i x_i - a_{ii} x_i^2 - \frac{a_{ij} x_i x_j}{1 + a_i x_i + \tilde{a}_j (x_j - 1)} \quad i \neq j, \quad i, j = 1, 2. \quad (4)$$

The model analyzed in [4] is (4) with $\tilde{a}_j = 0$. Here, instead, we are aimed to understand the *net effect* of intra-species interference when competing heterospecifics. Thus, we consider that the inter-species interference in competition is negligible, so that $a_i = 0$ and system (4) becomes

$$x'_i = r_i x_i - a_{ii} x_i^2 - \frac{a_{ij} x_i x_j}{1 + \tilde{a}_j (x_j - 1)} \quad i \neq j, \quad i, j = 1, 2. \quad (5)$$

The analysis of the complete model (4) is beyond the scope of this contribution and will be available somewhere. We rewrite system (5) accordingly to $u_i = a_{ii} x_i / r_i$, $c_{ij} = a_{ij} r_j / (r_i a_{jj})$, and $K_i = r_i / a_{ii}$, that yields

$$u'_i = r_i \left(u_i - u_i^2 - \frac{c_{ij} u_i u_j}{1 + \tilde{a}_j (K_j u_j - 1)} \right), \quad i \neq j, \quad i, j = 1, 2. \quad (6)$$

where c_{ij} is the competitive strength as defined in the left hand side of (3), K_i is the carrying capacity, and a_{ii}/r_i is the absolute competition coefficient [6] of species, $i = 1, 2$. It is clear that $\tilde{a}_j = 0$ in (5) yields the classical system (1). Assuming $\tilde{a}_j > 0$ gives rise to a new model, the competition model with Beddington-DeAngelis competitive response.

3 Results

We analyze system (6) by assuming that $0 < \tilde{a}_i < 1$ for $i = 1, 2$. From now on we assume that $r_i > 0$ for $i = 1, 2$, which implies that the trivial equilibrium point $E_0^* = (0, 0)$ is unstable. Thus, in the absence of species j , species i behaves according to the logistic equation

$$u_i' = r_i u_i (1 - u_i), \quad (7)$$

and $u_i^* = 1$ (that is equivalent to $x_i^* = r_i/a_{ii}$, the corresponding carrying capacity) is a global attractor for the solutions of (7).

A first result states that the dynamics of system (5) evolves eventually in the region $[0, 1] \times [0, 1]$:

Proposition 1. *The non-negative cone is invariant for system (6). Besides, any solution of such a system with positive initial values will eventually enter the region $[0, 1] \times [0, 1]$ and will not leave it.*

Proof. It follows from direct calculations using the fact that the solution of $u_i' = r_i(u_i - u_i^2)$ upper bounds the solution of the corresponding equation in system (6).

Indeed,

Proposition 2. *The solutions of system (6) converge eventually monotonically to an equilibrium point.*

Proof. It follows from direct calculations computing the conditions stated in [10].

Proposition 3. *Consider the semi-trivial equilibrium points. $E_1^* = (1, 0)$ and $E_2^* = (0, 1)$. Then, E_j^* is locally asymptotically stable if $c_{ij} > \tilde{c}_{ij}^*$ for $i \neq j$, $i, j = 1, 2$ respectively, where*

$$\tilde{c}_{ij}^* = 1 + \tilde{a}_j(K_j - 1), \quad i = 1, 2, \quad i \neq j. \quad (8)$$

Proof. The existence of E_i^* follows from direct calculations. The stability conditions follow from a standard analysis of the eigenvalues of the Jacobian matrix.

We next classify the possible outcomes of system (6) in terms of the coefficients of the model. It will turn out that the quantities

$$\Gamma_i = \frac{1 + \tilde{a}_i(K_i - 1)}{\tilde{a}_i K_i} = 1 + \frac{1 - \tilde{a}_i}{\tilde{a}_i K_i}, \quad i = 1, 2 \quad (9)$$

play a key role. Note that $K_i \geq 1$ since they are carrying capacities. Indeed, we divide the $c_{12}c_{21}$ positive cone into four regions

$$\begin{aligned}
 R_{coex} &:= \{0 < c_{12} < \tilde{c}_{12}^*, 0 < c_{21} < \tilde{c}_{21}^*\} \\
 R_{pe} &:= \{\tilde{c}_{12}^* < c_{12}, \tilde{c}_{21}^* < c_{21}\} \\
 R_1 &:= \{0 < c_{12} < \tilde{c}_{12}^*, \tilde{c}_{21}^* < c_{21}\} \\
 R_2 &:= \{\tilde{c}_{12}^* < c_{12}, 0 < c_{21} < \tilde{c}_{21}^*\}
 \end{aligned} \tag{10}$$

that define the possible outcomes of system (6) (see Figure 2).

Proposition 4. *Consider system (6). Then:*

1. *Global coexistence. There exists an equilibrium point in the non-negative cone that is GAS for any $(c_{12}, c_{21}) \in R_{coex}$.*
2. *Priority effects. There exists a saddle equilibrium point in the non-negative cone that is unstable for any $(c_{12}, c_{21}) \in R_{pe}$. Indeed, E_1^* and E_2^* are locally asymptotically stable, and the stable manifold of the positive (component-wise) equilibrium defines the basins of attraction of each semi-trivial equilibrium point.*

Proof. The non-trivial equilibrium points are the solutions to the equation resulting from equating the nullclines of system (6). The number of solutions included in the non-negative cone follows from applying the Descartes' rule of signs to that equation. The stability conditions of the semi-trivial equilibrium points E_1^* and E_2^* were proved in Proposition 3. The stability of the non-trivial equilibrium points follows from the above considerations and Proposition 2.

Proposition 5. *Consider system (6). Then:*

1. *Assume now that $\Gamma_1 = \Gamma_2$, that is*

$$\frac{K_2}{K_1} = \frac{\tilde{a}_1(1 - \tilde{a}_2)}{\tilde{a}_2(1 - \tilde{a}_1)} \tag{11}$$

Then, it follows that:

- (a) *Species 1 wins: E_1^* is GAS whenever $(c_{12}, c_{21}) \in R_1$.*
 - (b) *Species 2 wins: E_2^* is GAS whenever $(c_{12}, c_{21}) \in R_2$.*
2. *Instead, if $\Gamma_1 < \Gamma_2$, that is equivalent to*

$$\frac{K_2}{K_1} < \frac{\tilde{a}_1(1 - \tilde{a}_2)}{\tilde{a}_2(1 - \tilde{a}_1)} \tag{12}$$

Then, it follows that:

- (a) *Species 1 wins: E_1^* is GAS whenever $(c_{12}, c_{21}) \in R_1$.*
- (b) *Consider the second degree equation on u_1 that raises from equating the nullclines of system (6). Then, there exists a curve, Ψ_+ , arising from solving on c_{21} the result of equating to zero the discriminant of the solution of the above-mentioned second degree equation such that*

i. Species 2 wins: E_2^* is GAS whenever

$$\{(c_{12}, c_{21}) \in R_2\} \cap \{(c_{12}, c_{21}); c_{21} < \Psi_+(c_{12})\} \quad (13)$$

ii. Conditional coexistence in favour of species 2. On the contrary, if

$$\{(c_{12}, c_{21}) \in R_2\} \cap \{(c_{12}, c_{21}); \Psi_+(c_{12}) < c_{21}\} \quad (14)$$

then E_2^* is locally asymptotically stable and E_1^* unstable. In addition, there exist two equilibrium points in the positive cone, one locally asymptotically stable and one unstable. The latest is a saddle equilibrium point whose stable manifold separates the basins of attraction of E_2^* and the positive (coexistence) equilibrium point.

3. Finally, if $\Gamma_1 > \Gamma_2$, that is equivalent to

$$\frac{K_2}{K_1} > \frac{\tilde{a}_1(1 - \tilde{a}_2)}{\tilde{a}_2(1 - \tilde{a}_1)} \quad (15)$$

Then, it follows that:

(a) Species 2 wins: E_2^* is GAS whenever $(c_{12}, c_{21}) \in R_2$.

(b) Consider the second degree equation on u_1 that raises from equating the nullclines of system (6). Then, there exists a curve, Ψ_- , arising from solving on c_{21} the result of equating to zero the discriminant of the solution of the above-mentioned second degree equation such that

i. Species 1 wins: E_1^* is GAS whenever

$$\{(c_{12}, c_{21}) \in R_1\} \cap \{(c_{12}, c_{21}); \Psi_-(c_{12}) < c_{21}\} \quad (16)$$

ii. Conditional coexistence in favour of species 1. On the contrary, if

$$\{(c_{12}, c_{21}) \in R_1\} \cap \{(c_{12}, c_{21}); c_{21} < \Psi_-(c_{12})\} \quad (17)$$

then E_1^* is locally asymptotically stable and E_2^* unstable. In addition, there exist two equilibrium points in the positive cone, one locally asymptotically stable and one unstable. The latest is a saddle equilibrium point whose stable manifold separates the basins of attraction of E_1^* and the positive (coexistence) equilibrium point. See the right panel of Figure 3.

Proof. When equating the nullclines of system (6) we get a second degree equation for u_1 . The solutions of such an equation are the u_1 component of the equilibrium points of system (6). Letting the discriminant of the solution of that equation equal to zero, the curves Ψ_+ and Ψ_- are obtained. These curves bound the regions on the $c_{21}c_{12}$ plane where there are two, one or none equilibrium points (that is, the algebraic equation has either real or complex solutions).

Signs of the coordinates of the equilibrium points are determined by using the Descartes' rule of signs. The number of equilibrium points inside the non-negative cone, in addition with stability of the semi-trivial equilibrium points (Proposition (2)) yield the stability of the non-trivial equilibrium points.

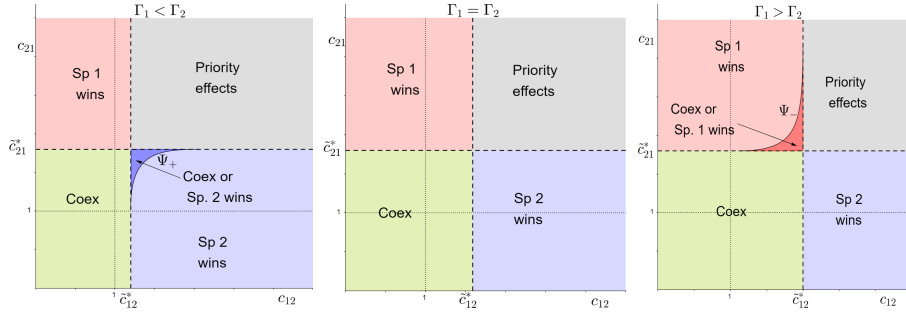


Fig. 2: Competition outcomes of system (6) as function of the competitive strengths c_{12} , c_{21} for increasing values of $\tilde{a}_2 = 0.1, 0.3, 0.5$ (from left to right). Other parameter values are: $r_1 = 6.8$, $r_2 = 2$, $K_1 = 5$, $K_2 = 3$, $\tilde{a}_1 = 0.2$. The code colour is the same as in Figure 1 except for the dark blue and dark red regions, that represent conditional coexistence in favour of species 2 or 1, respectively. Note $\tilde{a}_1 = 0.2$ is kept fixed in the three figures and \tilde{a}_2 varies. As a consequence, \tilde{c}_{21}^* remains the same while \tilde{c}_{12}^* varies accordingly. Fixing \tilde{a}_2 and varying \tilde{a}_1 would let fixed \tilde{c}_{21}^* and change \tilde{c}_{12}^* .

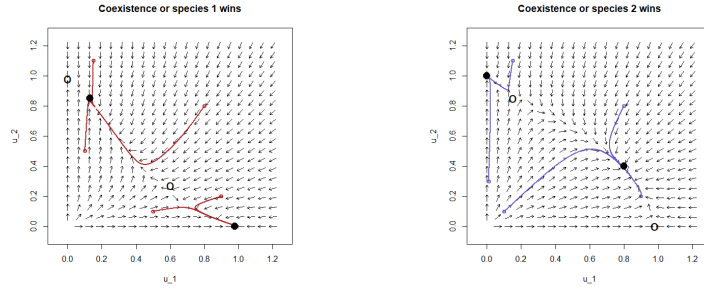


Fig. 3: Conditional coexistence in favour of species 1 (left panel, either species 1 wins or there is species coexistence) or species 2 (right panel, either species 2 wins or there is species coexistence).

4 Discussion

It is intuitive that spending time on interfering with conspecifics softens the competitive effect on heterospecifics. In this work we are able to translate into numbers such a consequences as described in Proposition 4.

Qualitatively, the new dynamical scenarios are equivalent to those found in the recent literature. However, the driving process is different: it is not interference between heterospecifics [4], neither group defense [5] or herd behavior [13] nor the result of a competitive-cooperative balance [15].

A key result is that the global coexistence region is larger than that in [1], [4], [5], [13] or [15]. This feature constitutes an explanation (not unique) of the Paradox of Coexistence. Also, conditional coexistence (items 2b) and 3b) in Proposition 5) expands the scenarios permitted by the classical model allowing for coexistence.

It is of full interest to analyze system (4) for $a_i > 0$ and $\tilde{a}_i > 0$ to fully understand the combined effect of interfering with con- and hetero-specifics when competing.

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